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The Genus *Pterodrilus* (Annelida: Branchiobdellida)

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The branchiobdellid worms, once greatly neglected, have received somewhat more attention in recent years. Occurring as epizoites on freshwater decapods and, in a few cases, on other crustaceans of the Northern Hemisphere, their distribution, evolution, and relationships with their hosts furnish several interesting problems. In spite of increased interest in them, however, the systematic account of no genus of North American branchiobdellids is at a stage adequate for a satisfactory consideration of many of these broader problems.

Such is the case for the genus *Pterodrilus*, whose members form a distinctive part of the branchiobdellid fauna of eastern North America. In the last 20 years, however, I have gathered together a large number of specimens of the previously known species of the genus plus material representing five new species.

It is now possible, therefore, to present a more nearly adequate definition of the genus, redescriptions and new distributional data for the previously described species, descriptions of the new species, and a discussion of the evolutionary and geographical relationships of the genus. These are the objectives of the present paper.

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METHODS AND DISPOSITION OF MATERIAL.—The material used in this study that was collected by persons other than Mrs. Holt and myself was collected and preserved in 70% ethyl alcohol. My collecting methods and procedures have been described elsewhere (Holt, 1960a, p. 57). Except for some paratypes of new species and a small number of specimens retained for reference purposes in my collections at the Virginia Polytechnic Institute, the material is deposited in the collections of the United States National Museum. Where appropriate, United States National Museum catalog numbers (USNM) and my personal catalog numbers (PCH) are listed with the locality data given for a species. In all cases, complete locality data are available from my files or from the Registrar, United States National Museum. The terminology used in branchiobdellid taxonomy and evaluation of the taxonomic utility of various characters have also been discussed previously and the reader is referred to these papers (Holt, 1953, 1960a, Holt and Hoffman, 1959), but some relevant explanations and anatomical comparisons are presented, where appropriate, in discussions of certain species.

REVIEW OF THE LITERATURE.—Knowledge of the genus *Pterodrilus* dates from Moore's paper entitled "*Pterodrilus*, a remarkable discodrilid" (Moore, 1895a). He separated the genus from previously known branchiobdellids (="discodrilids" of authors, e.g., Vejdovsky, 1884) on the basis of the striking dorsal "appendages" of the two species (*P. alcicornus* and *P. distichus*) that he described and assigned to his new genus. His descriptions are excellent for the state of knowledge of the branchiobdellids of his time, and his species are easily recognized. Since then, Pierantoni (1912, pp. 24–25) and Stephenson (1930, p. 801) mentioned the genus in their literature survey. Ellis (1918, pp. 49–51), by means of a key, assigned his species *durbini* to *Pterodrilus;* subsequently (1919, pp. 254–255), he formally described and illustrated *P. durbini*, described *P. mexicanus*, and listed new locality records for

P. distichus. Goodnight (1940, pp. 58–63) quoted the original descriptions of the four nominal species of *Pterodrilus* and added a new locality record for *P. durbini*. Later, he recorded the presence of *P. alcicornus* in Sinking Creek, Giles County, Va. (Goodnight, 1941b, p. 468). A new species was recognized and previously known ones of the genus were redescribed in my unpublished dissertation (Holt, 1951, pp. 100–148). Later I reassigned *P. durbini*, placing it in the newly established genus *Ellisodrilus* (Holt, 1960b, pp. 173–176). Recently, *P. alcicornus* and its distribution have been discussed (Hobbs, Holt and Walton, 1967, pp. 61, 71, 73–74). Causey (1955, p. 44) recorded the presence of *P. mexicanus* in Arkansas. Other than passing references (e.g., Hoffman, 1963, pp. 294, 295) or mention in various keys, nothing else has been written about the genus *Pterodrilus* by North American authors. In Europe, however, Moszyński (1937, pp. 71–72; 1938, pp. 99–103) and Georgévitch (1955, pp. 200–203; 1957, p. 14) described species that they had assigned to *Pterodrilus*, but Pop (1965, pp. 223–225) pointed out the obvious fact that these European species were based upon material belonging to the genus *Branchiobdella* and synonomized them with *B. parasita* Henle, 1835. They are as follows: *Pterodrilus karamani* Moszyński, 1937; *Pterodrilus bidens* Georgévitch, 1955; *Pterodrilus megas* Georgévitch, 1955; *Pterodrilus prion* Georgévitch, 1955; *Pterodrilus megodont* Georgévitch, 1955; *Pterodrilus aliata* Georgévitch, 1957; *Pterodrilus dantata* Georgévitch, 1957.

Pterodrilus Moore, 1895

Type-species.—*Pterodrilus alcicornus* Moore, 1895a, pp. 449–450, by subsequent designation (Goodnight, 1940, p. 58).

Diagnosis.—Small branchiobdellids (known forms less than 2.0 mm in length) of delicate appearance; cylindrical; prosomite of segment VIII always with elevated dorsal ridge, those of other segments often so, dorsal ridges often bearing fan- or finger-like projections; jaws delicate, light in color or colorless, triangular in shape, dental formula 5/4; prostate present, incompletely divided from spermiducal gland; bursa ovoid to pyriform, penis sheath short, penis non-eversible; spermatheca with long ectal duct, bulb clavate or spatulate; anterior nephridia open by common dorsal pore on segment III.

Affinities.—The close relationship of the species of *Pterodrilus* to those of *Cambarincola* has been discussed earlier (Hoffman, 1963, pp. 294–295), and the exclusion of the species at present assigned to *Cambarincola* from the older genus *Pterodrilus* has elements of arbitrariness that require discussion.

Part of the argument for maintaining the generic staus of the two groups of closely related species is based upon a conservative desire

to preserve nomenclatural stability. The genus *Cambarincola*, as presently understood, is composed of, by far, the largest number of species of any genus of the order Branchiobdellida. With the exception of the Eurasian genus *Branchiobdella*, it has the greatest geographical range of any genus now known. In almost all localities where they occur, the species of *Cambarincola* are the dominant elements of the branchiobdellid fauna. To transfer all these species to the much less well-known and smaller genus *Pterodrilus* could result only in a period of nomenclatural confusion.

This argument alone, however, cannot justify excluding the species now assigned to *Cambarincola* from *Pterodrilus*. Moore was struck with the unusual appearance of *P. alcicornus* and *P. distichus* with their ornamentation of dorsal projections, and he established a new genus for them. Although he described the male reproductive system of both species (Moore, 1895a, pp. 453, 454), the importance of this system to the systematics of the branchiobdellids was not appreciated at that time, nor, indeed, by Ellis who did, however, present a diagram of it in his paper establishing the genus *Cambarincola* (Ellis, 1912, p. 483).

The difficulty arises from the fact that the basic plan of the reproductive system of species of *Pterodrilus* does not differ from that of the members of *Cambarincola* as much as it does from other genera of the order. Recent workers (Holt, 1960a, 1960b, 1967a, 1967b, Hoffman, 1963; Laing, 1963) have derived their generic concepts from the major variations in pattern of the male reproductive system, and I regard these variations as furnishing the most usable characters for marshalling groups of species into genera. Also, the jaws of species of *Pterodrilus* are quite similar in shape and arrangement of the teeth to those of species of *Cambarincola*. But the jaw patterns are shared by two or more genera in other cases, and the jaws of all species of *Pterodrilus* are of essentially the same form.

We have, however, in *Pterodrilus* a group of distinctive species that obviously belong together as a specialized offshoot from the main direction of the evolution of *Cambarincola*. A formal diagnosis obscures by its brevity and technical language the distinctiveness of such a group. The species of *Pterodrilus* are smaller than those of *Cambarincola* and are characteristically delicate in appearance. The jaws are correspondingly reduced in size and pigmentation. Always there are ridges on some of the segments and usually these ridges bear projections. It is true that both segmental ridges, produced by supernumerary muscles (Holt, 1960b, p. 172), and projections of various sorts occur in other genera and that several species of *Cambarincola* have such ridges. None of the latter species, however, are easily confused with those of *Pterodrilus*. The male reproductive systems of species of *Pterodrilus* vary, but the spermiducal gland is relatively short and

thick and the prostate is less completely divided from the spermiducal gland than in any species of *Cambarincola*.

The dorsal projections of such species as *P. alcicornus*, *P. distichus*, *P. mexicanus* and three of the five new species described herein readily set them apart from *Cambarincola*. There would be no difficulty in maintaining the generic separateness of these species except for the last two of the new species treated herein, which are closely related to the others but lack fan- or finger-like projections on the ridge of segment VIII. This is not unexpected: the species assigned to *Pterodrilus* are believed to have arisen from a generalized stock of *Cambarincola* as animals adapted to a niche that favored a reduction in size and the production of the ridges and their projections.

The species of *Pterodrilus* are a distinct group that might be placed within a larger group which includes the species assigned at this time to *Cambarincola*. Since, however, generic status has been accorded these two groups for many years, I prefer to retain both names and assign such taxa as the new species without dorsal projections to one or the other of the existing genera on the basis of judgments as to the closeness of affinities with species previously assigned to them. There are precedents for such decisions in many groups; for instance, among the hosts of the branchiobdellids, the genera *Procambarus* and *Orconectes* are united by intermediate species that must be assigned rather arbitrarily to either genus (Hobbs, 1967, p. 8).

One species, *P. durbini* Ellis (1919, pp. 254–255), previously assigned to *Pterodrilus* has been removed from the genus and referred to the genus *Ellisodrilus* Holt (1960b, pp. 173–176). *Ellisodrilus* is one of a group of genera related to *Cambarincola* and hence to *Pterodrilus*. It differs from *Pterodrilus* in the absence of a spermatheca and the asymmetry and other unique features of the bursa. *Ceratodrilus*, *Oedipodrilus*, and *Magmatodrilus* are other related genera. *Magmatodrilus* Holt (1967b) lacks a prostate, the bursa is proportionally quite large and there are no dorsal projections; the penial sheath of *Oedipodrilus* is elongated, enclosing an eversible penis, the prostate is relatively very small and dorsal projections are absent (Holt, 1967a, p. 58); *Ceratodrilus* Hall (1914, p. 191) is composed of larger worms in which the prostate is extremely reduced in size and the penis is eversible (Holt, 1960a, p. 57).

Distribution.—The genus *Pterodrilus* is confined to eastern North America including Mexico. Within this area there are three distinct centers of distribution: the Southern Appalachians with adjacent portions of the Interior Plateau east of the Mississippi River and the glaciated region north of the Ohio River to the Great Lakes and the Saint Lawrence River; the Ozarkian uplift

north of the Arkansas River in Arkansas, Missouri, and Oklahoma; the eastern slopes of the Sierra Madre Oriental in Veracruz. Obviously, this fragmented range must at some time have been continuous. A discussion of possible migration routes and the evolution of the genus follows the systematic accounts.

Key to the Species of Genus *Pterodrilus*

1. Dorsal projections present 3
   Dorsal projections absent, prosomite of segment VIII raised 2
2(1). Dorsal ridges on segments I–VIII . . . . . **P. missouriensis,** new species
   Dorsal ridge on segment VIII only . . . . . **P. choritonamus,** new species
3(1). Dorsal projections on raised prosomite of segment VIII only 4
   Dorsal projections on raised prosomites of other segments in addition to segment VIII 6
4(3). Segments I–VIII with ridges . . . . . **P. cedrus,** new species
   Segments other than VIII without ridges 5
5(4). Fanlike dorsal projection of segment VIII with 5 prongs; bursa small, ejaculatory duct long . . . . . **P. hobbsi,** new species
   Fanlike dorsal projection of segment VIII with 4 prongs; bursa large, ejaculatory duct short . . . . . **P. mexicanus** Ellis
6(3). Two finger-like dorsal projections on segments II–VII, 5 on segment VIII . . . . . **P. distichus** Moore
   Fanlike dorsal projections on segments III–V, VIII 7
7(6). Fanlike dorsal projection lacking on segment II . . . **P. alcicornus** Moore
   Fanlike dorsal projection present on segment II . . . **P. simondsi,** new species

Pterodrilus alcicornus Moore

FIGURES 1, 10

Pterodrilus alcicornus Moore, 1895a, pp. 450–453.—Pierantoni, 1912, p. 25.—Ellis, 1919, p. 254.—Goodnight, 1940, pp. 58–50; 1941, p. 468.—Hobbs, Holt, and Walton, 1967, pp. 61–62.

TYPE-SPECIMENS.—The material from Johns River, Watauga County, N.C., upon which Moore based this species, has not been found among Moore's collections now in the U.S. National Museum nor among the collections of the Academy of Natural Sciences of Philadelphia. The species is distinctive, subsequent identifications are not disputed, and no neotype has been designated.

DIAGNOSIS.—Dorsal ridges on segments II–VIII; those of III–V, VIII bearing fanlike dorsal projections; bursa ovoid, less than ½ body diameter in length; ejaculatory duct of medium length; length of spermiducal gland about 3 times its diameter; prostate subequal in diameter to that of spermiducal gland and ½ to ⅔ its length, histologically differentiated from the latter; spermatheca longer than body diameter, bending dorsad to gut, ectal duct long and narrow, bulb clavate, ental process absent.

DESCRIPTION.—The length of individuals of *Pterodrilus alcicornus* (based on 10 specimens) is about 1.3 mm. The head is slender, its length about ⅛ that of the body and its diameter about ½ that of the greatest body diameter. The intersegmental grooves of the head, except for that setting off the peristomium, are indistinct.

The trunk or body is cylindrical throughout and increases gradually in diameter up to the reproductive segments (V–VII), which are all essentially the same diameter (about 0.25 mm). The sucker, formed from segment XI, is subequal to or slightly greater than the head in diameter.

The dorsal appendages or projections are borne on ridges of the prosomites. In *P. alcicornus*, they are paired lobes that diverge somewhat and extend laterally and anteriorly in the case of the anterior three to form forward-facing concavities. The projection of segment VIII is similar, except that it faces posteriorly. The lobes ("wing-like" projections) bear conical prongs, usually three on each side, although the number varies from one to four prominent prongs, with smaller ones frequently present. The lobes of the projection of segment V do not flare out quite so much as do those of the others and the prongs project more nearly upward. Dorsal ridges are present on the prosomites of segments VI and VII.

The spermiducal gland is thick for its length, with a length-diameter ratio of about 3:1. In length and diameter, the prostate is about ¾ of these dimensions of the spermiducal gland though it often appears in whole mounts to be subequal in diameter to that of the latter. The prostate is differentiated. The ejaculatory duct is about ½ the length of the bursa and slightly expanded along its midlength. The diameter of the bursa is approximately ¾ its length. The bursal glands mentioned by Moore (1895a, p. 454) are not present. He described as glands the fold of the wall of the bursal atrium that becomes the "rim of the cup" of the everted bursa.

The ectal duct of the spermatheca is long and slender, widening gradually into the bulb, which is also long and bends over the gut dorsally; the total length of the spermatheca exceeds the body diameter. There is no ental process of the spermatheca though the ental end of the bulb may resemble such a process when incompletely filled with spermatozoa.

DISCUSSION.—The following account of the anatomy of *P. alcicornus* is a condensation of my unpublished earlier treatment (Holt, 1951, pp. 101–115). Serial sections were used as well as whole mounts and the earlier observations confirmed by more recent examination of many specimens. The abundance of this material affords an opportunity to describe *P. alcicornus* is some detail and, thereby, present

a treatment of the anatomy of the species that will serve to introduce the reader more fully to features common to all species of the genus and as a basis for the shorter descriptions of the other species of *Pterodrilus* that follow.

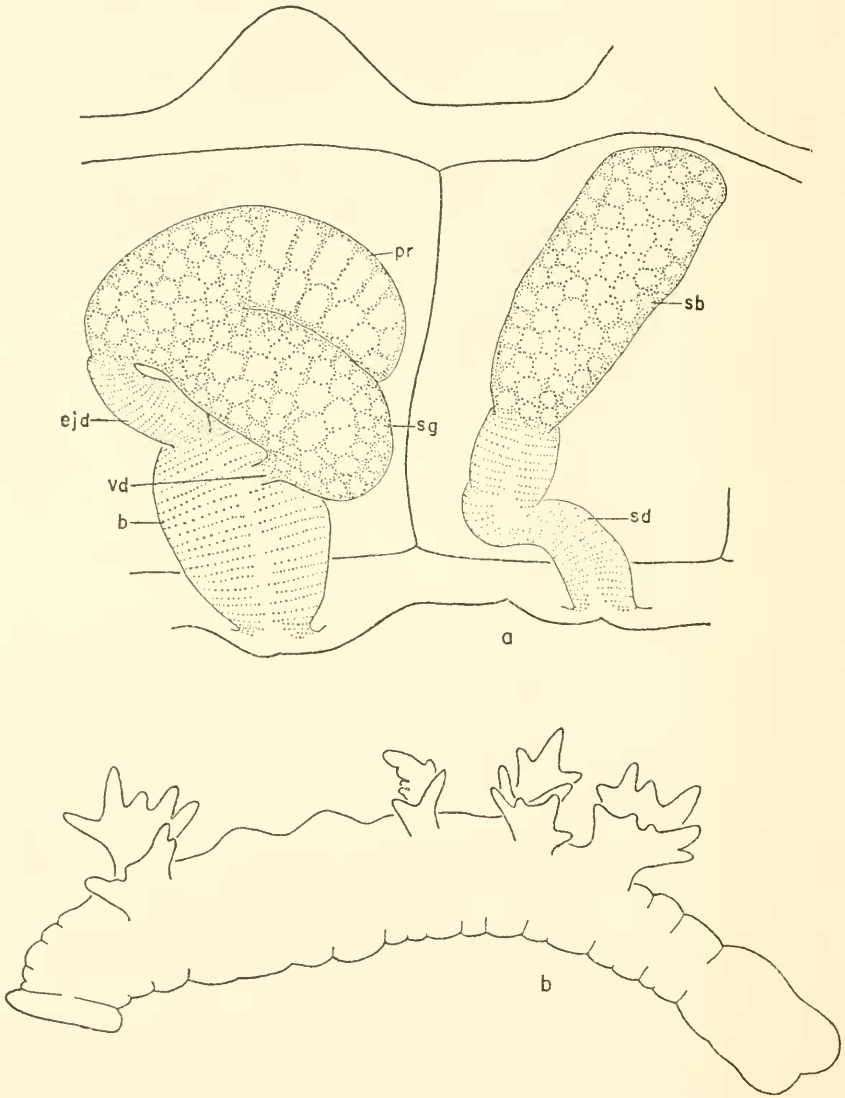

FIGURE 1.—*Pterodrilus alcicornus*: *a*, lateral view of reproductive systems; *b*, animal from Giles County, Va. (b=bursa; ejd=ejaculatory duct; pr=prostate; sb=bulb of spermatheca; sd=spermathecal duct; sg=spermiducal gland; vd=vas deferens.)

The dorsal ridges, which may bear projections in *P. alcicornus* and other species of *Pterodrilus* and may occur without projections in species of other genera, are formed by the attachment of muscles ("supernumerary muscles," Holt, 1960b, pp. 171–172) that are shorter than the segment to the cuticle and that, by their contraction, differentially shorten the dorsal surface of the prosomites in which they occur. There has been no suggestion by anyone, nor is it indicated in their structure, as to the function of the dorsal projections. They consist of flat "wing-like" or cylindrical "finger-like" (prongs) extensions of the epidermis covering the dorsal ridges. The wall of the projections is a single-cell-layer thick (as is the epidermis) with unicellular glands as a prominent feature. The interior of the projections is an irregular cavity that does not appear to communicate with the coelom. The finger-like projections are usually set off by a slight constriction. Dorsal ridges that are present on segments VI and VII do not bear projections on these reproductive segments in any species of the genus.

Since the jaws of all species of *Pterodrilus* are monotonously similar, they have not been illustrated for all the species included in this study (see, however, figs. 2, 4, 5, 7). They are small, delicate and light yellowish brown (but see p. 11, below). The upper jaw bears five sharply pointed teeth, the lower four (dental formula 5/4); and they are more nearly quadrate in shape than is usual among species of *Cambarincola* with the same dental formula. Moore (1895a, p. 425) believed both jaws of *P. alcicornus* to be quadridentate, but this was probably because of the smallness of the lateral teeth of the upper jaw, which may cause one of them to be overlooked.

All branchiobdellids possess two pairs of nephridia and the anterior pair may open by either separate pores or by a common pore on the dorsum of segment III. The anterior nephridia of *Pterodrilus* and related genera open by a common pore, which in *P. alcicornus* is located at the base anteriorly of the dorsal projection. The nephridiopore usually cannot be seen in animals mounted entire, but there is little doubt that this arrangement is consistently present in *Pterodrilus*.

The innermost parts of the branchiobdellid male reproductive system consist of testes in segment V or in segments V and VI, a pair of sperm funnels and sperm ducts (vasa efferentia) in each testicular segment, and a vas deferens from each of these segments that is formed by the union of the sperm ducts. These elements are quite similar throughout the order and will not be described here (but see Moore, 1895b, pp. 519–521; Holt, 1949, pp. 538–541, 550–552).

The spermiducal gland is formed by the union of the vasa deferentia and does vary in shape and structure. Other than its peritoneal

covering and a very thin layer of circular muscles, the gland consists of a tube composed of a single layer of columnar epithelium, the individual cells of which open into a narrow lumen. All of these gland cells are filled with granules though differences in the secretory cycle of individual cells can be detected in sectioned material. There are no apparent differences in the histological appearance of the spermiducal gland of *P. alcicornus* and the other species of *Pterodrilus* and that previously described for a species of *Cambarincola* (Holt, 1949, p. 552).

The prostate is a glandular diverticulum of the spermiducal gland that lies along the anteriodorsal border of the latter, ends blindly entally and opens either into the spermiducal gland somewhere along its ectal portion or with it into the ejaculatory duct. In *P. alcicornus* and the other species of *Pterodrilus*, the prostate opens into the spermiducal gland somewhat entally to the junction with the ejaculatory duct; that is, it is incompletely divided from the former. The prostate is of the same basic structure as the spermiducal gland from which it arises, but in *P. alcicornus* its glandular epithelium consists of highly vacuolated cells with different staining properties from those of the spermiducal gland. This histological difference between the two glands is readily apparent in well-prepared whole mounts and is present in all mature individuals of species of *Pterodrilus* with the exceptions mentioned below (pp. 16, 25). The expressions "differentiated" and "undifferentiated" are used to distinguish between such prostates as those of *P. alcicornus* and those that are histologically like the spermiducal gland in both sectioned material and whole mounts. In many species of the genus *Cambarincola*, the ental end of the prostate consists of a thin-walled bulb, the interior of which is a cavity (Holt, 1949, p. 553; 1960a, p. 63). There is no prostatic bulb in *P. alcicornus*.

The ejaculatory duct is a muscular tube which is found in most branchiobdellids and unites, if present, the spermiducal gland and the copulatory bursa. That of *P. alcicornus* is not unlike that of other species of the genus except in length.

The copulatory bursa of *P. alcicornus* and other species of the genus is quite similar to that of members of the genus *Cambarincola*. The penial sheath region of the bursa in *P. alcicornus* is not demarcated externally from the bursal atrium and composes about half of the organ. When the atrial portion of the bursa is everted, the penis is protruded as a short and relatively slender tube surrounded by the cuplike everted bursal atrium. More detailed descriptions of the type of bursa found in the species of *Pterodrilus* may be found in Holt (1949, pp. 553–555) and Hoffman (1963, pp. 289–290).

The ovaries and ovipores of all branchiobdellids seem to be basically similar (Moore, 1895b, pp. 524–525; Holt, 1949, pp. 545–547, 560).

The spermatheca, however, does vary. The length and diameter of both the ectal duct and bulb may differ among the species of *Pterodrilus;* the bulb may be thin walled as it is in *P. alcicornus* and many other branchiobdellids (Holt, 1949, p. 560, fig. 18), and an ental process may be present. The terms used for these parts of the spermatheca are defined in Holt (1960a, p. 64).

The organ systems of *P. alcicornus* and its congeners, with the exception of those discussed above, are not noticeably different from those of other branchiobdellids.

Variations.—The foregoing description and discussion of *P. alcicornus* is based primarily upon specimens from the New River drainage in Virginia. Differences in methods of killing and preservation, that is, the use of dilute solutions of alcohol, produce some distortion of the specimens. There is little of note in the way of intrapopulational variation, except for differences in the number of prongs of the dorsal projections. A count of these for 10 specimens from Giles County, Va., gave the following results:

segment III	*segment* IV	*segment* V	*segment* VIII
5	4	5	7
7	6	6	7
5	5	5	7
7	5	5	7
6	6	5	6
8	7	7	7
7	5	5	6
7	5	5	6
5	3	4	5
5	5	3	5

Similar results were obtained from specimens from other parts of the range of the species.

The "wings" of the dorsal projections of at least some specimens from the Watauga River system in North Carolina and Tennessee and the headwaters of the New River in North Carolina are of greater extent than those of specimens from other parts of the species' range. The latter material, however, is poorly preserved, which may account for the apparent differences.

The jaws of some specimens from Alleghany County, N.C., are much darker than usual. That this may reflect something other than geographical variability is indicated by the presence of dark jaws in at least one collection from Giles County, Va., where most specimens have lightly colored jaws.

The extent of variability in the species is not enough, or at least it is not well enough defined geographically, to allow one to consider the erection of subspecies.

Affinities.—*Pterodrilus alcicornus,* in external appearance, is

most like *P. simondsi* and *P. distichus*. It differs from both in the absence of dorsal projections on segment II and from *P. distichus* in the fanlike instead of finger-like nature of the projections. The reproductive systems of *P. alcicornus* differ in only minor details, mostly in length and shape of the spermatheca, from those of *P. hobbsi* and *P. distichus* and in the fully differentiated prostate and thin-walled spermathecal bulb from *P. simondsi*.

HOSTS.—*Pterodrilus alcicornus* was found with the following crayfishes: *Cambarus sciotensis* Rhoades, *C. bartonii bartonii* (Fabricius), *C. robustus* Girard, *C. bartonii* subspecies, *C. longulus longirostris* Faxon, *C. longulus chasmodactylus* James, *Cambarus* species, *Orconectes juvenilis* Hagen, *Cambarus parvoculus* Hobbs and Shoup, *C. bartonii cavatus* Hay, *C. veteranus* Faxon, *C. acuminatus* Faxon, *C. longulus longulus* Girard, *Orconectes sanborni sanborni* (Faxon). The most frequent hosts are *C. sciotensis* and *C. bartonii bartonii*.

DISTRIBUTION.—*Pterodrilus alcicornus* is widespread in the streams of the Tennessee and New Rivers in Tennessee, North Carolina, and Virginia. In addition, it has moved—apparently recently since it is not common there—into other adjacent drainages: the Savannah River in Transylvania County, N.C., the James River drainage in Craig County, Va., the Roanoke River drainage in Franklin and Patrick Counties, Va., the Big Sandy River drainage in Buchanan and Dickenson Counties, Va., and Wyoming County, W. Va. (fig. 10). Most of my collections of *P. alcicornus* are from Virginia, and the greater number of known localities for the species in the New River drainage in Virginia may be, but probably is not, a peculiarity of collecting. The range as given here may not be complete for it is possible that *P. alcicornus* occurs in other adjoining drainages.

MATERIAL EXAMINED.—Several hundred specimens from 122 collections were studied. The bulk of this material is deposited in the U.S. National Museum (USNM 36184–36250).

Pterodrilus distichus Moore

FIGURES 2, 10

Pterodrilus distichus Moore, 1895a, pp. 453–454.—Pierantoni, 1912, p. 25.—Hall, 1914, pp. 190, 193.—Ellis, 1919, p. 254.—Goodnight, 1940, pp. 60–61; 1943, p. 100.

TYPE-SPECIMENS.—The material from western New York, upon which Moore based this species, has not been found. The species is distinctive, subsequent identifications are not disputed, and no neotype has been designated.

DIAGNOSIS.—Low, somewhat indistinct ridges on segments I–VIII, those of segments II–VII each with two bluntly pointed cylindrical

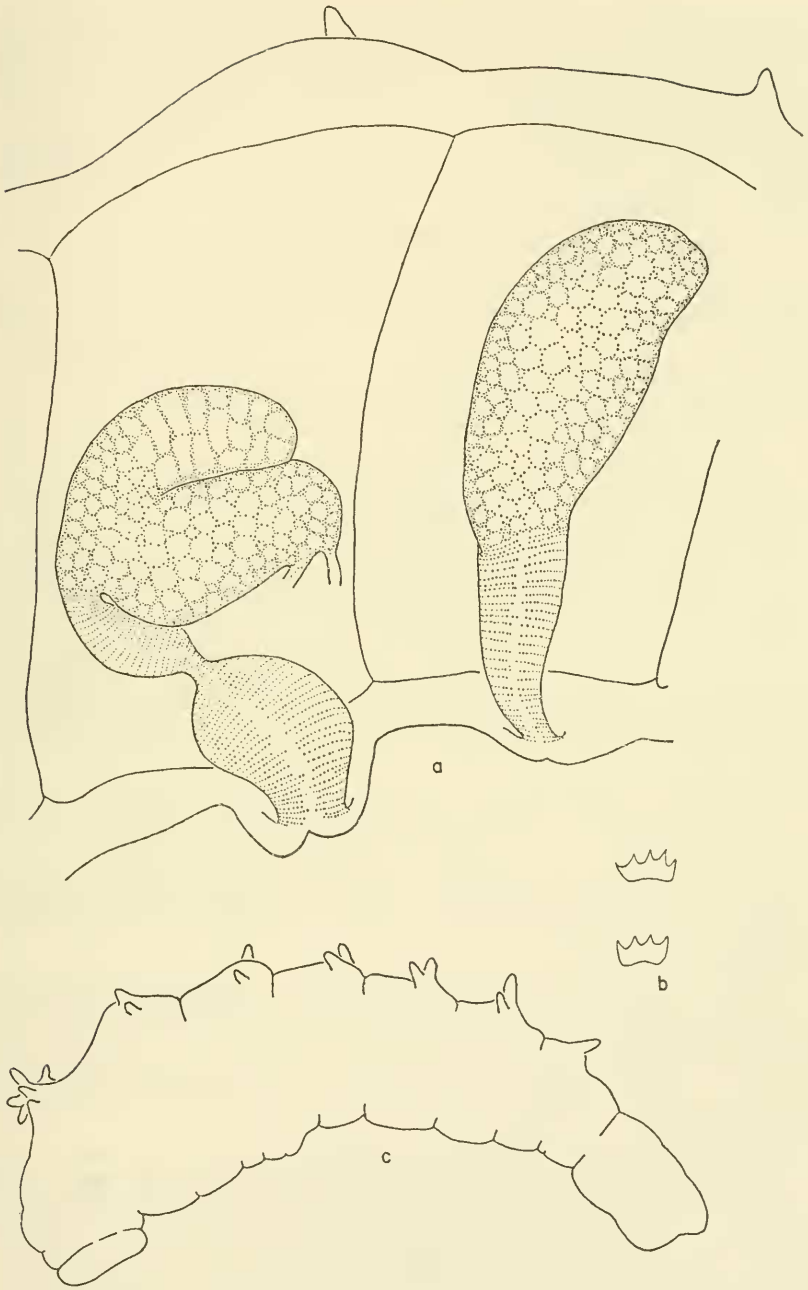

FIGURE 2.—*Pterodrilus distichus: a*, lateral view of reproductive systems; *b*, en face view of jaws, upper jaw above; *c*, animal from Seneca County, N.Y.

dorsal projections, that of segment VIII with five projections; bursa subspherical, small, hardly reaching ventral border of gut; ejaculatory duct of medium length; prostate broadly joined to spermiducal gland, subequal in length and diameter to latter, differentiated; spermiducal gland small, its length about twice its diameter; spermatheca clavate, length subequal to body diameter, ectal duct gradually merging into bulb, without ental process.

Description.—In size the members of this species differ very little from those of *P. alcicornus*, but are perhaps slightly larger, with an average length of 1.4 mm. The dorsal ridges would hardly attract attention if they did not bear projections. The latter are relatively short and about $\frac{1}{10}$ the greatest body diameter in length. There are two of these on segments II–VII and five on segment VIII.

The spermiducal gland, ejaculatory duct, bursa, and penis differ from those of *P. alcicornus* only in their smaller size.

The spermatheca is not proportionally as long as that of *P. alcicornus* and does not bend appreciably over the gut although its length is approximately equivalent to the body diameter; the ectal duct appears to be somewhat wider than that of *P. alcicornus* and is not greatly different in diameter from the bulb at the union of the two.

Variation.—Minor differences that may be noted in the size of specimens, the length of the dorsal projections, and the size and proportions of the reproductive systems perhaps are best correlated with differences in age or nutrition and in the methods of killing and preserving.

Affinities.—The differences between *P. distichus* and *P. alcicornus* have been noted (p. 12). The two species are closely related. In the number of dorsal appendages, *P. distichus* agrees with *P. simondsi*, but the reproductive systems of these two species are significantly different (p. 25).

Hosts.—*Pterodrilus distichus* has been associated with *Orconectes propinquus* (Girard), *O. immunis* (Hagen), *O. obscurus* (Hagen), *O. juvenilis* (Hagen), *O. rusticus rusticus* (Girard), *Cambarus robustus* Girard, *C. bartonii bartonii* (Fabricius) and *C. longulus chasmodactylus* James, of which the two most frequent hosts are *O. propinquus* and *C. robustus*.

Distribution.—*Pterodrilus distichus* has been taken from the states of New York, Ohio, Kentucky, Indiana, Illinois, and Michigan (fig. 10). All of these records are from regions covered by ice during the Wisconsin glaciations except those from Breathitt, Madison, Jessamine, and Harrison Counties, Ky. The first three of these Kentucky records are from the Kentucky River drainage, the last from the Licking River system, both streams of the Ohio drainage. The conclusion is that the ancestors of *P. distichus* have moved from some-

where near the Kentucky River across the Ohio into the glaciated areas of the Ohio-Mississippi and Great Lakes drainage systems since the melting of the Wisconsin glacier.

Material Examined.—Approximately 200 specimens from 25 collections have been examined. Specimens from all these collections are deposited in the U.S. National Museum (USNM 17651–17653, 36160–36183).

Pterodrilus mexicanus Ellis

Figures 3, 9

Pterodrilus mexicanus Ellis, 1919, p. 254.—Goodnight, 1940, p. 63.—Causey, 1955, p. 44.

Type-specimen.—Holotype, USNM 17654, from Mirador, Veracruz, Mexico. Host: *Cambarus mexicanus* Erichson; Nelson and Goldman, collectors.

Diagnosis.—Dorsal ridge on segment VIII, typically bearing four conical projections, remainder of segments without ridges; bursa large, elongate, length exceeding ½ body diameter; ejaculatory duct short; prostate about ½ diameter of and subequal in length to spermiducal gland, undifferentiated; spermatheca shorter than body diameter, bulb thick walled.

Description.—*Pterodrilus mexicanus* differs externally from other species of *Pterodrilus* in the arrangement and number of the dorsal ridges and projections. There are no ridges present, except that on segment VIII, which has four finger-like, conical projections, very similar to those of *P. distichus*. The total length averages 1.1 mm.

The spermiducal gland is about three times its diameter in length and lies along the upper border of the gut. The prostate, subequal in length to and about half the diameter of the spermiducal gland, is histologically undifferentiated in most specimens although some specimens show a vacuolation of some cells along its ental and dorsal borders. The ejaculatory duct is very short. The bursa, however, is large, about 1½ times longer than that of *P. alcicornus* and 3 times that of *P. distichus*. This great increase in size is primarily accounted for by an increase in the length of the atrial area, which is not only larger but has additional inwardly directed folds of the bursal wall. The penial sheath region and the penis itself is as in other species of *Pterodrilus*. Specimens with the bursa everted have not been seen; but one would expect a cup-within-a-cup structure to be produced by eversion.

The spermatheca of *P. mexicanus* is shorter than that of most species of the genus, hardly extending above the upper border of the gut. The inner part of the ectal duct is often enveloped in an expanded ectal part of the bulb. The blind end of the spermatheca frequently

resembles an ental process, except that often it is distended with spermatazoa. The wall of the spermathecal bulb is thicker than in all other species of the genus except *P. simondsi*.

VARIATION.—One or two specimens have only three dorsal projections on segment VIII instead of four. The length of the prongs vary, those of the type are larger than those of most specimens. This difference appears to be of sporadic occurrence and of no systematic importance. The prostate of some specimens is partially vacuolated (cf. *P. simondsi*, p. 25, below).

AFFINITIES.—*Pterodrilus mexicanus* is related to *P. missouriensis*, *P. choritonamus*, *P. cedrus*, and *P. hobbsi*. In features of the reproductive system, *P. mexicanus* is most similar to *P. missouriensis*. These two Ozarkian species differ in that in *P. mexicanus* the ejaculatory duct is short, the bursa is larger, the prostate is partially differentiated, the spermatheca is shorter and the wall of the spermathecal bulb is thicker, and there are no dorsal ridges on segments I–VII. The absence of dorsal ridges except on segment VIII ally *P. mexicanus* with *P. hobbsi*, a more advanced member of the same lineage (see below, p. 36), which differs from *P. mexicanus* in the fully differentiated prostate, long ejaculatory duct, small bursa, and thin-walled spermathecal bulb. *Pterodrilus mexicanus* shares the absence of dorsal ridges, except on segment VIII, with *P. choritonamus*, which, however, lacks projections on this dorsal ridge. In addition, the latter species differs from *P. mexicanus* in that the bursa is smaller, the ejaculatory duct is longer, the prostate is differentiated, and the spermatheca has an ental process. *Pterodrilus cedrus* belongs in the same lineage as *P. missouriensis* and differs from *P. mexicanus* in the presence of dorsal ridges on segments I–VII, a smaller, more nearly spherical bursa, a longer ejaculatory duct, a differentiated prostate, and a longer spermatheca without an ental process.

HOSTS.—*Pterodrilus mexicanus* has been taken from 10 species of the genus *Orconectes: O. punctimanus* (Creaser), *O. ozarkae* Williams, *O. meeki meeki* (Faxon), *O. neglectus neglectus* (Faxon), *O. nana nana* Williams, *O. nais* (Faxon), *O. luteus* (Creaser), and *O. hylas* (Faxon).

DISTRIBUTION.—Two of my collections are from the Arkansas River drainage in northwestern Arkansas and eastern Oklahoma; four are from the St. Francis River system in Missouri; the remainder are from the White River drainage in Arkansas and Missouri. All of these streams, however, drain the Ozark highlands centered in south-central Missouri. The range of *P. mexicanus*, thus, is compact and well delimited except for the type-locality, Veracruz, Mexico.

MATERIAL EXAMINED.—Approximately 100 specimens from 22 collections from Arkansas, Missouri, and Oklahoma were studied.

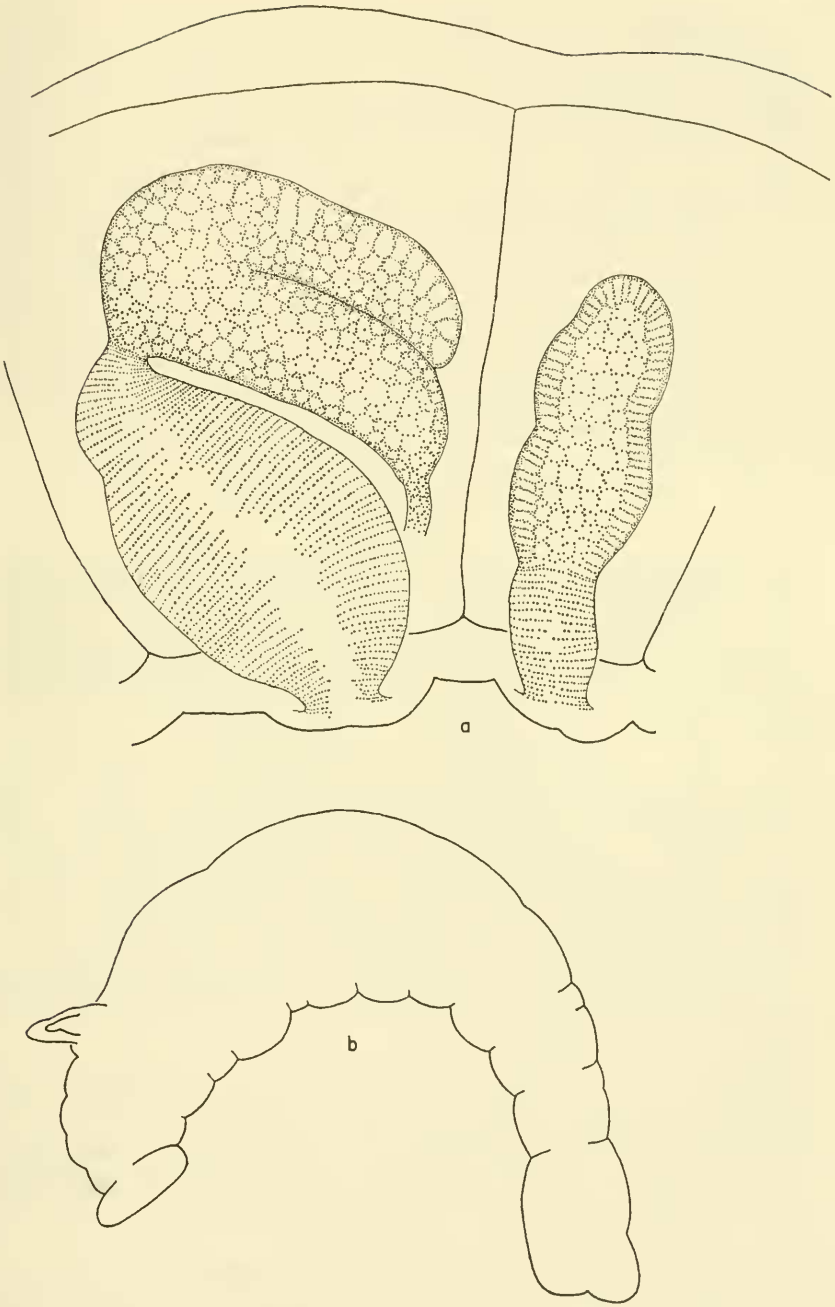

FIGURE 3.—*Pterodrilus mexicanus: a*, lateral view of reproductive systems; *b*, animal from Wayne County, Mo.

This material, for the most part, is deposited in the U.S. National Museum (USNM 36138–36159).

Remarks.—The holotype of *P. mexicanus* Ellis (1919) from Mirador, Veracruz, Mexico, is poorly preserved, making a study of the internal structures impossible; it was separated from other branchiobdellids by Ellis (1919, p. 254) on the sole basis of the "simple four-horned appendage like that on the same segment of *P. distichus*." I have collected branchiobdellids in Mexico and unsuccessfully have tried to locate Mirador. Among the 64 collections from Mexico that I have studied, there are no specimens that can be assigned to the genus *Pterodrilus*. I have, therefore, with considerable hesitation, referred my material from the Ozarks to *P. mexicanus*. The possibility remains that a future discovery of *P. mexicanus* at or near the type-locality will necessitate the renaming of the Ozarkian animals.

Pterodrilus hobbsi, new species

Figures 4, 9

Type-specimens.—Holotype, USNM 36486, and five paratypes, USNM 36487, from *Cambarus rusticiformis* Rhoades, *Orconectes juvenilis* (Hagen), and *O. placidus* (Hagen) taken from Spring Creek, 1.4 miles north of the Putnam County line on State Highway 43, Overton County, Tenn., by Perry C. and Virgie F. Holt, July 26, 1961.

Diagnosis.—Dorsal ridge present on segment VIII, bearing fanlike projection with five prongs, other segments without dorsal ridges and projections; bursa small, ovoid, length less than half body diameter; ejaculatory duct of normal length; spermiducal gland relatively large; prostate about ¾ diameter of and subequal in length to spermiducal gland; spermatheca clavate, bending dorsally over gut.

Etymology.—I take great pleasure in naming this species in honor of Dr. Horton H. Hobbs, Jr., as a token of my gratitude for the many years of friendly help he has given me in my study of the branchiobdellids.

Description.—In shape and size, *P. hobbsi* is much like other members of the genus, differing from all except *P. choritonamus* and *P. mexicanus* in the absence of ridges on the prosomites of all segments except the eighth. The dorsal projection of this segment is fanlike and bears five tapering prongs of which the median is the longest. The length ranges from about 1.3 to 1.7 mm.

The spermiducal gland is not markedly different from that of *P. mexicanus;* the prostate, however, is distinctly vacuolated; that is, it is histologically differentiated, but there is no distinct prostatic bulb. The two organs are broadly joined and often the spermiducal

gland lies so that the true extent and appearance of the prostate is obscured. The ejaculatory duct is markedly longer than that of the unusually short one of *P. mexicanus* and is expanded along its mid-length. The bursa is small and ovoid, intermediate in size between those of *P. alcicornus* and *P. distichus*, and much smaller that of *P. mexicanus*.

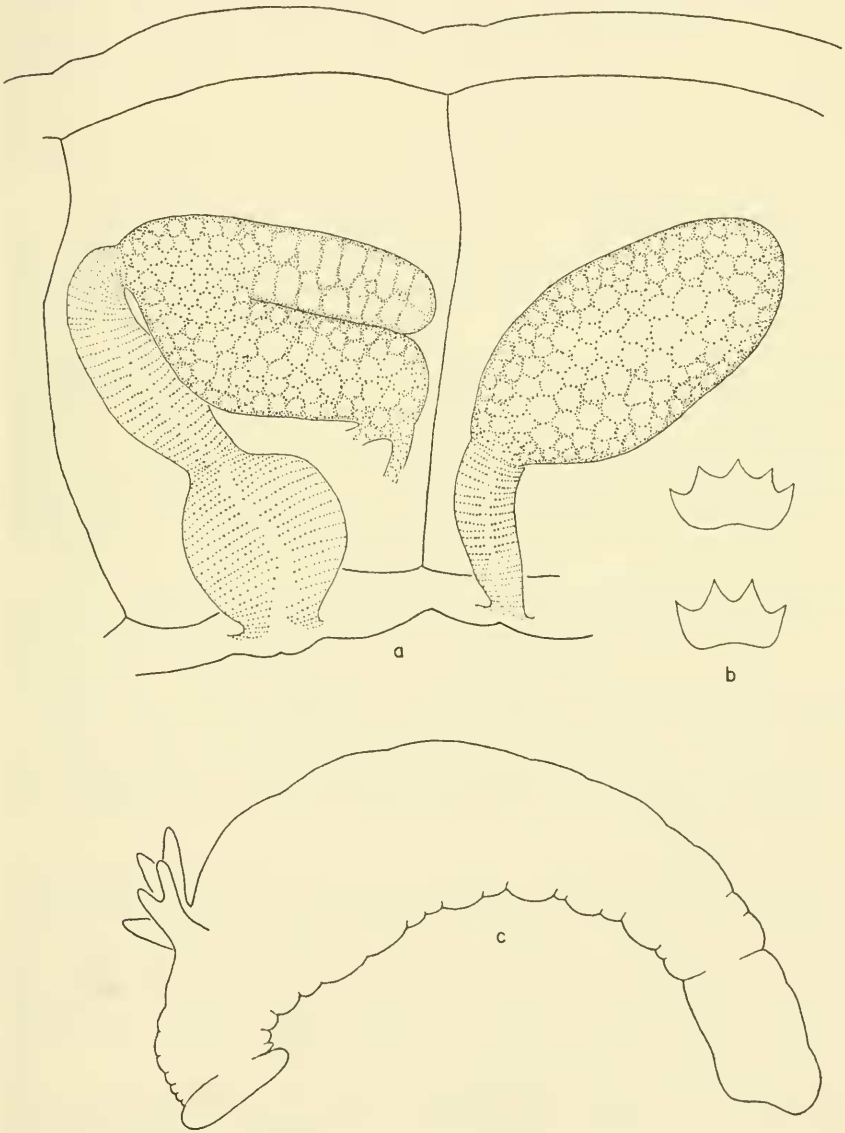

FIGURE 4.—*Pterodrilus hobbsi:* *a*, lateral view of reproductive systems; *b*, en face view of jaws, upper jaw above; *c*, animal from Lee County, Va.

The spermatheca is quite similar to that of *P. distichus*, perhaps slightly broader along the midlength of the bulb. It is approximately as long as the body diameter and bends dorsad over the gut. The ental end is composed of larger cells and in many specimens there is a small ental process.

VARIATION.—The prongs of the dorsal projections vary in length, but this may be related in part to differences in the degree of contraction. The reproductive organs show only minor differences in apparent shape and proportions—except for the prostate, which appears to be variable in length, and the extent of vacuolation. The ectal portion near its junction with the spermiducal gland is often not differentiated, but in all individuals the blind end is vacuolated to a greater extent and more consistently than in *P. mexicanus*.

AFFINITIES.—*Pterodrilus hobbsi* is similar to *P. choritonamus* and *P. mexicanus* in the absence of dorsal ridges on all segments except the eighth, but it differs from both of these species in the smaller bursa and from *P. mexicanus* in the presence of five instead of four prongs of the dorsal projections and in the consistently differentiated prostate (see p. 16). The reproductive systems are most like those of *P. distichus* and *P. alcicornus*, species with dorsal projections on several segments.

HOSTS.—*Pterodrilus hobbsi* has been taken in association with 17 species and subspecies of *Cambarus* and 4 species of *Orconectes: Cambarus tenebrosus* Hay, *C. longulus longirostris* Faxon, *C. parvoculus* Hobbs and Shoup, *C. longulus chasmodactylus* James, *C. robustus* Girard, *C. veteranus* Faxon, *C. friaufi* Hobbs, *C. extraneus* Hagen, *C. bartonii cavatus* Hay, *C. sciotensis* Rhoades, *C. distans* Rhoades, *C. bartonii bartonii* (Fabricius), *C. longulus longulus* Girard, *C. latimanus* (LeConte), *C. striatus* Hay, *Cambarus* species, *C. bartonii* subspecies; *Orconectes erichsonianus* (Faxon), *O. juvenilis* (Hagen), *O. rusticus forceps* (Faxon), and *Orconectes* species. The most common hosts were *Cambarus longulus longirostris*, *C. bartonii cavatus*, and *Orconectes juvenilis*.

DISTRIBUTION.—*Pterodrilus hobbsi* inhabits most of the upper Tennessee drainage system and is especially common in tributaries of the Nolichucky, Watauga, Holston, Powell, and Clinch Rivers. It has also invaded the New River in Bland and Carroll Counties, Va., and Alleghany County, N.C.; the Big Sandy in Dickenson County, Va.; and is at home in a wide stretch of the Cumberland River drainage in Tennessee and Kentucky (fig. 9).

MATERIAL EXAMINED.—Types and over 300 specimens from 62 collections have been examined. The major part of this material is deposited in the U.S. National Museum (USNM 36488–36508).

REMARKS.—Unfortunately, much of the material on which the description of *P. hobbsi* is based is poorly preserved since it was collected by students of crayfishes whose requirements are such that the branchiobdellid material in their collections often proves unsuitable for careful study or positive identifications. There is no doubt that *P. hobbsi* is a distinct species occupying an extensive range; future studies based upon larger series of collections that are better preserved may reveal the presence of other and similar species among the animals presently assigned to this species (see below, p. 32).

Pterodrilus cedrus, new species

FIGURES 5, 10

TYPE-SPECIMENS.—Holotype and five paratypes, USNM 36464, from *Orconectes placidus* (Hagen) and *Cambarus tenebrosus* Hay taken in a small stream at the intersection of State Highways 52 and 53 at Celina, Clay County, Tenn., by Perry C. and Virgie F. Holt, July 25, 1961.

DIAGNOSIS.—Dorsal ridges on segments I–VIII, that of VIII bearing four short conical projections; bursa subspherical, small, reaching ventral border of gut; ejaculatory duct of medium length; prostate about ⅔ diameter of and equal in length to spermiducal gland, differentiated; spermatheca frequently exceeding body diameter in length, strap shaped to clavate, ectal duct long.

ETYMOLOGY.—Latin, *cedrus*, the cedar tree, by extension as a common name, the red cedar, *Juniperus virginiana*, for the cedar glades that are such a conspicuous part of the landscape of middle Tennessee.

DESCRIPTION.—*Pterodrilus cedrus* is a small worm, about 1.0 to 1.3 mm long; the combination of dorsal ridges on the first eight body segments and the four finger-like projections borne on the ridge of segment VIII are distinctive. These projections are short and resemble closely those of the corresponding segment of *P. distichus*.

The spermiducal gland is small, approximately twice its diameter in length. The prostate is broadly joined to the spermiducal gland and composed of highly vacuolated cells that end abruptly at the level of the separation of the two. It extends entally to the ental end of the spermiducal gland. The ejaculatory duct is about equal in length to the bursa and therefore longer than that of *P. mexicanus* and perhaps somewhat shorter, relative to the size of the organs, than that of *P. hobbsi*. The bursa is much like that of all members of the genus, except *P. mexicanus*, *P. choritonamus*, and *P. missouriensis*, that is, small and subspherical in shape.

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The spermatheca is long, with a long ectal duct. The bulb is elongate oval and usually bent mesiad over the gut dorsally. There is no ental

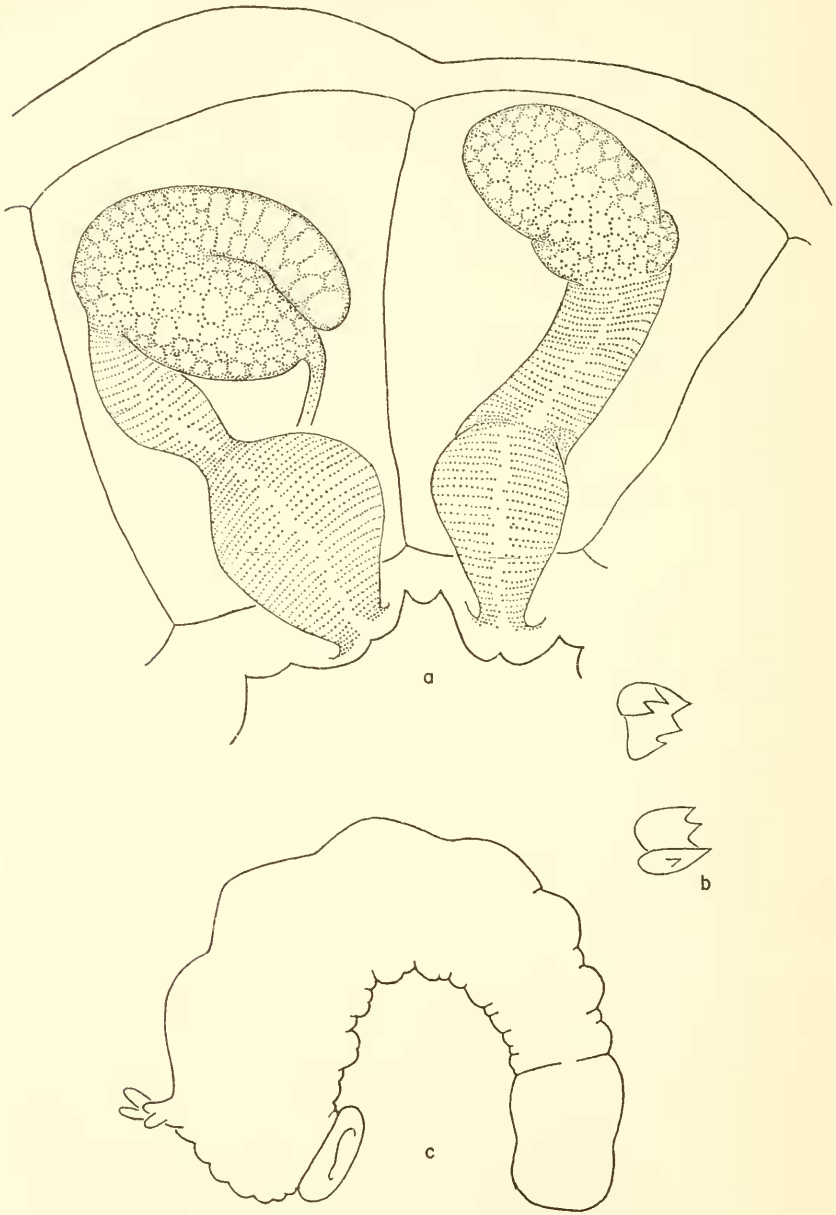

FIGURE 5.—*Pterodrilu cedrus: a,* lateral view of reproductive systems; *b,* oblique view of jaws; *c,* holotype.

process. The organ is narrower and the ectal duct is longer than is usual in the genus.

VARIATION.—Observable variability is confined to the spermatheca and seems to depend upon the degree of distension of the bulb with spermatozoa. When incompletely distended, there appears to be an ental process and the ectal duct is long; when fully distended, the ental process disappears and the ectal duct is shorter; that is, the ental part of the duct becomes part of the bulb. A cursory inspection might lead to the conclusion that there are structural differences of the spermatheca among individuals of the same population.

AFFINITIES.—*Pterodrilus cedrus* is superficially most like *P. hobbsi* but differs in having dorsal ridges on segments I–VIII, the shorter and finger-like dorsal projections of segment VIII instead of the fanlike projection with five prongs of the latter, the longer ectal duct of the spermatheca, and the narrower spermathecal bulb. The dorsal ridges of *P. cedrus* allies it, however, with the lineage culminating in *P. alcicornus*. Among these species (*P. simondsi*, *P. distichus*, and *P. alcicornus*), *P. cedrus* differs from *P. distichus* most markedly in the absence of two finger-like projections on the dorsal ridges of segments II–VII and the presence of four, instead of five projections on segment VIII.

HOSTS.—*Pterodrilus cedrus* has been taken with the following crayfishes: *Orconectes placidus* (Hagen), *O. rusticus* subspecies, *O. juvenilis* (Hagen) and *Cambarus tenebrosus* Hay.

DISTRIBUTION.—*Pterodrilus cedrus* is known only from a small series of collections taken in the eastern Highland Rim and Nashville Basin regions of Tennessee (fig. 10). Both its anatomical features and restricted distribution impute to it the status of a phylogenetic relict.

MATERIAL EXAMINED.—Types and 37 additional specimens. With the exception of three paratypes (PCH 1396) from the type-locality, this material is deposited in the United States National Museum (36465–36468).

Pterodrilus simondsi, new species

FIGURES 6, 10

TYPE-SPECIMENS.—Holotype, USNM 36477, five paratypes, USNM 36478, from *Cambarus bartonii bartonii* (Fabricius) taken in a tributary to the Ocoee River, 12.2 miles south of Morganton, on State Highway 60, Fannin County, Ga., by Kenneth W. Simonds, Nov. 6, 1958; four paratypes, PCH 989, from *Cambarus bartonii bartonii* taken in a tributary to the Ocoee River, 8.8 miles south of Morganton, Fannin County, Ga., on State Highway 60, by Kenneth W. Simonds, Nov. 6, 1958.

DIAGNOSIS.—Dorsal ridges on segments II–VIII, those of segments II–V, VIII bearing fanlike projections; bursa of medium size, with expanded atrial region; spermiducal gland relatively long, exceeding slightly anteroposterior dimension of segment VI in length; prostate ⅔ to subequal to spermiducal gland in diameter, subequal in length,

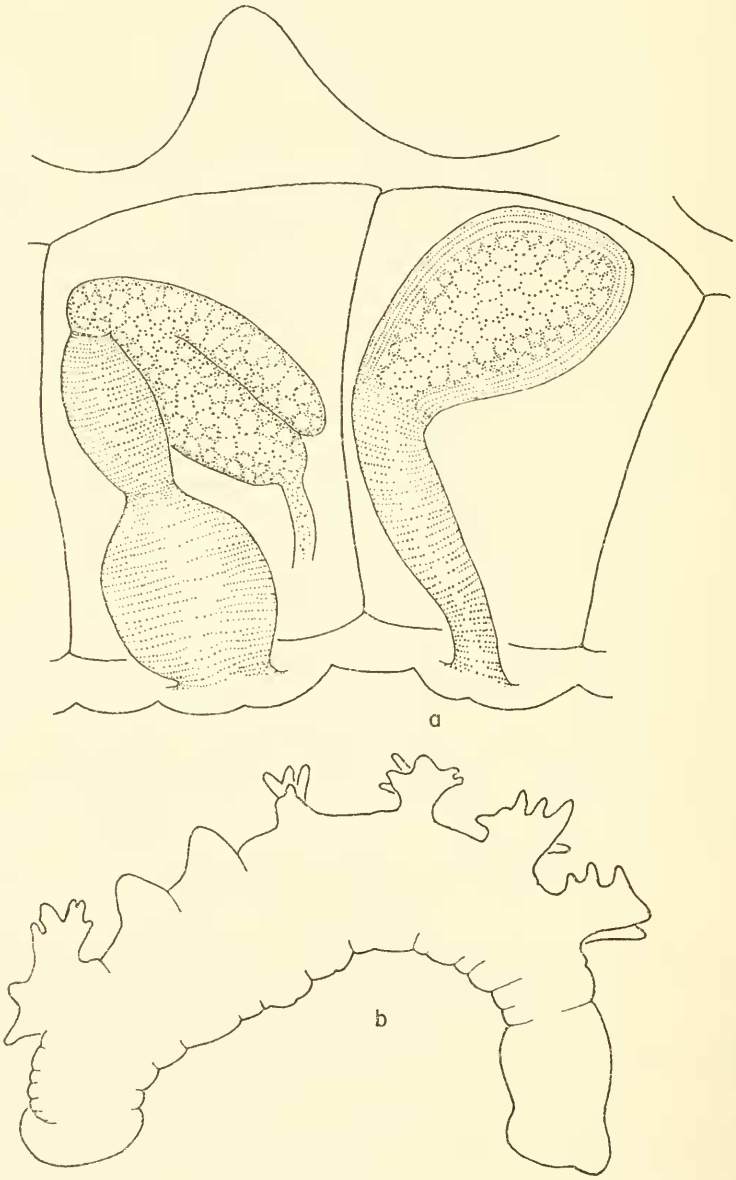

FIGURE 6.—*Pterodrilus simondsi: a*, lateral view of reproductive systems; *b*, holotype.

histologically differentiated in some specimens, not in others; spermatheca slightly longer than body diameter, ectal duct long, bulb clavate with thick muscular wall.

Etymology.—I am pleased to name this species in honor of its discoverer, Mr. Kenneth W. Simonds.

Description.—The dorsal ridges reach a greater height than in other species and more of them bear the expanded projections with prongs that may in turn be bifurcated or bear secondary prongs. The generalized description of the dorsal projections of segments III and VIII of *P. alcicornus* apply to those of segments II–IV and VIII of *P. simondsi*. The dorsal projection of segment V of *P. simondsi*, however, lacks the membranous lateral expansions of those of the other segments and are similar to the projections of segment VIII of *P. distichus*. *Pterodrilus simondsi* is composed of small worms about 0.9 to 1.3 mm long.

The bursa is smaller than that of *P. mexicanus*, but still larger, or at least longer, than is usual. The ejaculatory duct is prominent and rather noticeably expanded along its midlength. The spermiducal gland is somewhat longer than the anteroposterior dimension of the segment in which it lies and is usually oriented diagonally in the segment, extending dorsally above the gut. The diameter of the prostate ranges from ⅔ to subequal that of the spermiducal gland and extends entally to the ental end of the latter. It is more nearly separated from the spermiducal gland than in other species of the genus, the separation between the two extending almost to the junction of the spermiducal gland with the ejaculatory duct.

The spermatheca of *P. simondsi* is comparable in length and general shape to that of such species as *P. alcicornus* and *P. hobbsi*, but it differs in the heavier muscular investment of the bulb that distinctly persists even when the bulb is distended to the maximum with spermatozoa. There is no ental process.

Variation.—The only detectable variations in the material I have studied are those involving the prostate, which is, in some specimens, histologically identical to the spermiducal gland; in others it is composed of large, clear cells (vacuolated cells); and in still others some of the cells are composed of dense cytoplasm with many granules, and others are filled almost entirely with a clear material. In other words, in this species, the distinction between differentiated and undifferentiated prostates breaks down. The degree of distension of the spermathecal bulb is also variable. There can be no doubt that these are individual, intrapopulational variations.

Affinities.—*Pterodrilus simondsi* is closest in external appearance to *P. alcicornus*, from which it differs most noticeably in the presence of an additional dorsal projection on segment II, but the

reproductive systems of these two species are quite dissimilar. The prostate of *P. alcicornus* is always differentiated and its spermatheca lacks the muscular investment of the bulb characteristic of *P. simondsi*. *Pterodrilus simondsi*, then, is a less advanced member of a lineage derived from ancestors much like *P. missouriensis* and *P. cedrus* (see p. 21) that has also produced *P. distichus* and *P. alcicornus*.

Hosts.—The following crayfishes were found associated with *P. simondsi: Cambarus bartonii bartonii* (Fabricius), *C. latimanus* (LeConte) and *Cambarus* species. This is the only species of *Pterodrilus* for which no species of *Orconectes* is known to serve as a host (but see p. 32 below). Moreover, only once was it found in the absence of *C. b. bartonii*, the one record outside the Ocoee River, where it is associated with an unnamed species of *Cambarus*.

Distribution.—*Pterodrilus simondsi* is known only from the collections taken by Mr. Simonds from small tributaries to the Ocoee River in Fannin County, Ga., and Cherokee County, N.C., and one collection from a tributary to the Nottely River in Union County, Ga. In 1958–59 Mr. Simonds took 84 collections of crayfish from the Hiwassee River drainage to which the Ocoee and Nottely Rivers are tributary. Of his 19 stations in the upper Ocoee, *P. simondsi* was present at 14. The streams in which these stations were located are described as "small . . . with cold cascading waters, the bottoms of which are composed almost entirely of large flat stones often with several layers superimposed . . . . In such streams the water is clear even after heavy rains" (Simonds, unpubl. ms.). The thoroughness of Mr. Simonds' collecting efforts in similar streams of the Hiwassee River system to the north (75 collections, only one of which contained *P. simondsi*) leads to the conclusion that *P. simondsi* is a highly localized species. It should be searched for in the headwaters of the Savannah River to the east, the Chattahoochee River to the southeast, and the Coosa River to the southwest, but presumably *P. simondsi* is a relic of an early invasion of the area by primitive relatives of *P. alcicornus* that were adapted to cold, clear mountain streams.

Material examined.—Types and 53 specimens from 15 localities. The major part of this material is deposited in the U.S. National Museum (USNM 36479–36485).

Pterodrilus choritonamus, new species

Figures 7, 9

Type-specimens.—Holotype, USNM 36471, and two paratypes, USNM 36472, from *Cambarus tenebrosus* Hay taken in a tributary to

Eagle Creek (Holt Spring Branch) about 4.5 miles north of Livingston, Overton County, Tenn., by Perry C. and Virgie F. Holt, July 24, 1961; five paratypes, PCH 1393, from *Cambarus tenebrosus* and *Orconectes placidus* (Hagen) taken in Little Eagle Creek about 0.5 miles above confluence with Eagle Creek and about 6.0 miles north of Livingston, Overton County, Tenn., by Perry C. and Virgie F. Holt, July 24, 1961.

DIAGNOSIS.—Without dorsal projections, dorsal ridge present on segment VIII; bursa pyriform, small, extending at most to ventral border of gut; ejaculatory duct of medium length; prostate subequal to or shorter than spermiducal gland, diameter about ⅔ that of latter, differentiated; spermatheca with long ectal duct, median bulb and ental process.

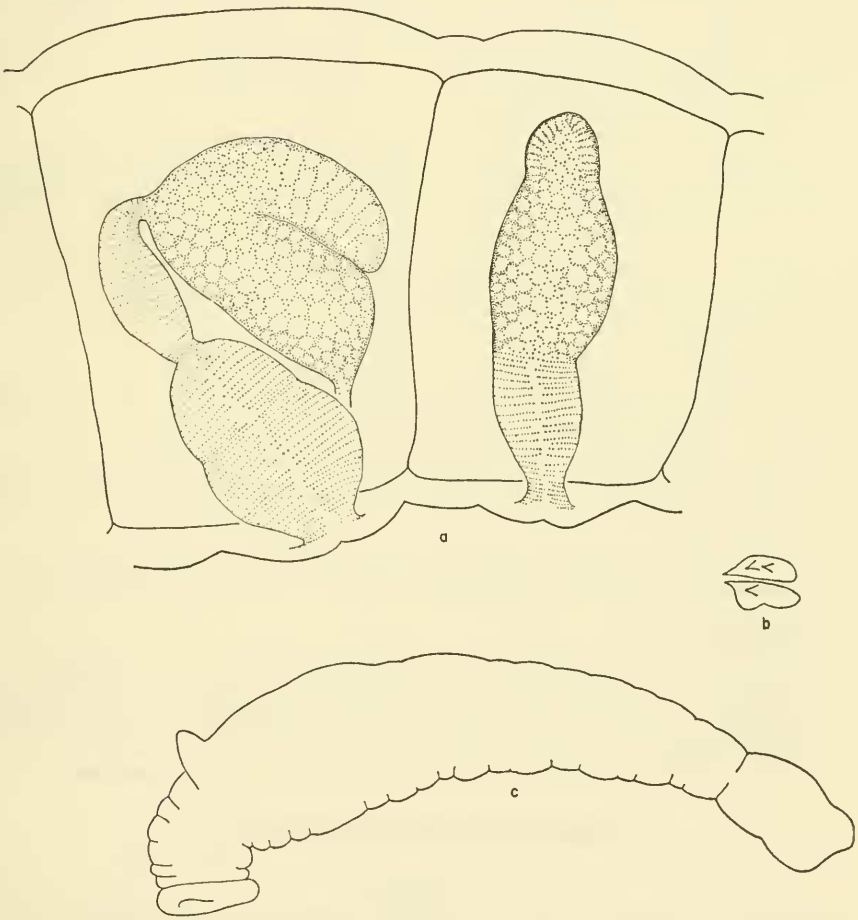

FIGURE 7.—*Pterodrilus choritonamus: a*, lateral view of reproductive systems; *b*, lateral view of jaws; *c*, holotype.

ETYMOLOGY.—From Greek, *choritos*, native, and *namos*, spring or stream, native spring, for the spring branch of my boyhood home.

DESCRIPTION.—*Pterodrilus choritonamus* is a small and delicate worm about 1.1 to 1.5 mm long. In body proportions and outline it is similar to *P. hobbsi* and *P. mexicanus*, differing in the absence of projections on the dorsal ridge of segment VIII.

The bursa approaches half the body diameter in length and is pyriform in shape: the penial sheath region is set off externally by a slight constriction and is less in diameter than the atrial portion of the bursa.

The spermatheca has the midlength of the organ (the spermathecal bulb) normally expanded, the ental portion not, so that there is an ental process that is lined with a columnar epithelium instead of a thin layer of flattened cells as is the bulb. Although the total length of the spermatheca is subequal to the body diameter, it is not as long as that of the other species of the genus except that of *P. mexicanus*, which it exceeds in length.

VARIATIONS.—The prostate varies in length, the ental end usually approaching the ental end of the spermiducal gland, but sometimes not. The spermatheca varies in the degree of the distension of the bulbular region, with the result that the extent of the ental process is reduced by a greater expansion of the bulb, but in the specimens I have seen the process is present and may, then, be a constant feature of the species.

AFFINITIES.—*Pteordrilus choritonamus* is related to *P. missouriensis*, *P. cedrus*, *P. mexicanus*, and *P. hobbsi*. Its affinities with the first three of these species have been discussed (p. 16). It differs from *P. hobbsi* in the absence of projections on the dorsal ridge of segment VIII, in the larger bursa and in having an ental process of the spermatheca.

HOSTS.—The known crayfish hosts of *P. choritonamus* are *Cambarus tenebrosus* Hay, *C. extraneus* Hagen, *Orconectes placidus* (Hagen) and *Orconectes* species.

DISTRIBUTION.—*Pterodrilus choritonamus* frequents tributaries of the Cumberland River in the Eastern Highland Rim in Tennessee.

MATERIAL EXAMINED.—Types and 28 specimens. The material for the most part is deposited in the United States National Museum (USNM 36473–36476).

Pterodrilus missouriensis, new species

FIGURES 8, 9

TYPE-SPECIMEN.—Holotype, USNM 36469, two paratypes, USNM 36470, and two paratypes, PCH 1476, from *Orconectes luteus* (Creaser)

taken in Whetstone Creek on U.S. Highway 60, 5 miles west of Mountain Grove, Wright County, Mo., by Perry C. Holt, August 23, 1961.

DIAGNOSIS.—Low dorsal ridges on segments I–VII, higher one on VIII, no dorsal projections; bursa large, its length equalling or ex-

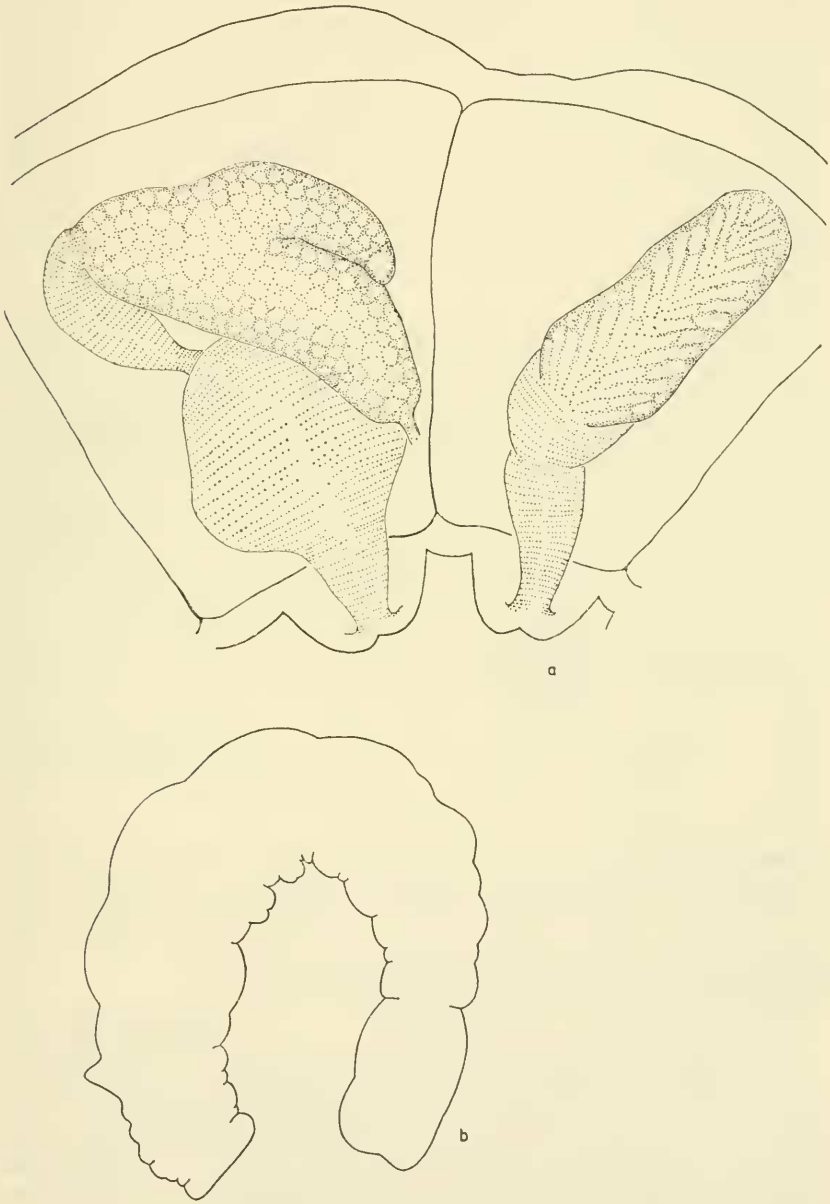

FIGURE 8.—*Pterodrilus missouriensis: a*, lateral view of reproductive systems; *b*, holotype.

ceeding ½ body diameter; spermiducal gland relatively long, its length equalling or exceeding anteroposterior dimension of seqment VI, narrowing at ectal end; prostate short, in diameter about ½ that of spermiducal gland, incompletely divided from latter, histologically undifferentiated, with ental bulb; spermatheca spatulate, its length subequal to body diameter, ectal duct long, ental process absent.

Etymology.—The adjectival form of Missouri.

Description.—The length, based on five animals, averages 1.6 mm (range 1.5–1.8 mm). The dorsal ridges of segments I–VII are poorly developed and in some extended specimens might be overlooked. That of segment VIII, however, is well developed. The anterior nephridiopore is clearly visible on the dorsum of segment III. The teeth of the jaws appear to be longer and more sharply pointed than is usual.

The male reproductive system in the totality of its primitive aspects, is unlike that of any other species of *Pterodrilus*. The spermiducal gland is relatively long and slender, its length more than three times its diameter. The prostate arises as a diverticulum of the gland rather far from the latter's junction with the ejaculatory duct. There is an abrupt narrowing at the point of origin of the prostate, from which point the spermiducal gland continues to decrease in diameter until it passes into the ejaculatory duct. The prostate has a diameter of about half that of the spermiducal gland and its ental end is located about ⅓ of the length of the latter from its ental end: in all, the prostate is about ⅓ the length of the spermiducal gland and lies along the median third of the gland. The prostate is not histologically differentiated, but there is an ental "bulb", a cavity of rather small extent. The ejaculatory duct is prominent and noticeably expanded along its midlength. The bursa is large, exceeding half the body diameter in length. The penis is prominent and the penial sheath region of the bursa is larger than usual.

The spermatheca has a long ectal duct that expands entally before it merges into the elongated, spatulate bulbular portion. There is no ental process, but in at least some specimens the entire wall of the bulb appears to be composed of large, granular cells with the result that the wall is much thicker than usual.

Variation.—The prostate appears to be of variable length, but this is probably because of the difficulty of estimating the comparative lengths of the prostate and spermiducal gland in specimens in which these organs are viewed from different directions. The ental part of the spermathecal bulb does not always appear to be filled with a glandular epithelium, but this is most likely a reflection of differences in degree of distension of the bulb with spermatozoa.

AFFINITIES.—*Pterodrilus missouriensis* is a primitive pterodrilid related to *P. choritonamus*, *P. mexicanus*, and *P. cedrus* (p. 21). It shares with *P. cedrus* the dorsal ridges of segments I–VIII but differs in the absence of projections on the dorsal ridge of segment VIII, the undifferentiated prostate, the shape of the spermiducal gland, the larger size of its bursa, and in the thicker-walled spermathecal bulb. *Pterodrilus missouriensis* and *P. choritonamus* both lack dorsal projections on segment VIII and have large bursae but differ in the presence of dorsal ridges on other segments, the undifferentiated prostate, the thicker-walled spermathecal bulb in the former, and an ental process

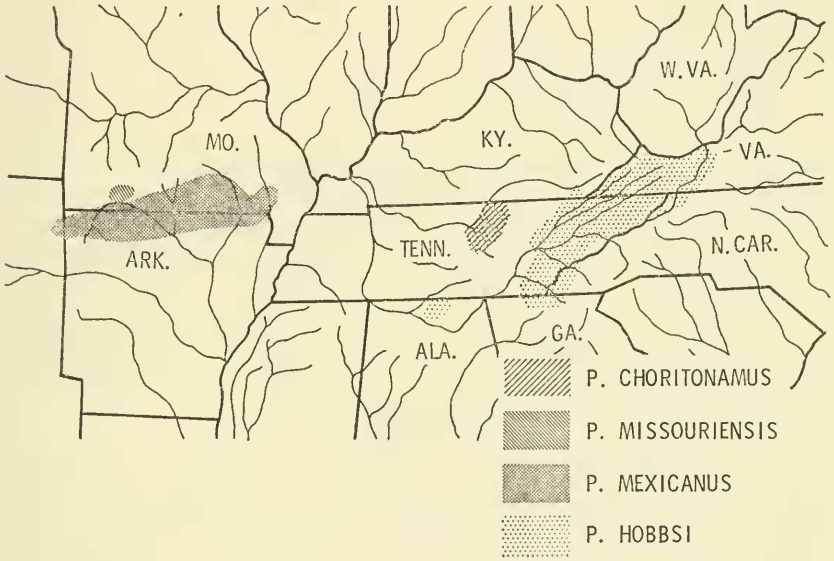

FIGURE 9.—Distribution of certain species of *Pterodrilus*.

of the spermatheca in the latter. *Pterodrilus missouriensis* shares with *P. mexicanus* the primitive nature of the prostate (p. 15) (though that of the latter is often partially differentiated), the large size of the bursa, and a spermatheca with a thicker-walled bulb; it differs from the latter in its much longer ejaculatory duct, the presence of dorsal ridges on segments anterior to segment VIII, and in the absence of dorsal projections.

HOSTS.—The only known host is *Orconectes luteus* (Creaser).

DISTRIBUTION.—*Pterodrilus missouriensis* is known only from the type locality, Whetstone Creek in Wright County, Mo. The one collection was taken from shallow pools in the headwaters of the stream, where there was little or no flow at an elevation of approximately 1260 feet. This locality is near the divide between the south-

ward-flowing White River drainage system and the northward-flowing Gasconade River and is a part of the latter system. There is no other record of a species of *Pterodrilus* from the Missouri River basin.

MATERIAL EXAMINED.—Five type-specimens.

Pterodrilus species

Poorly preserved material taken from three localities in the Hiwassee River drainage in Union County, Ga., and Cherokee County, N.C. (PCH 915, 974, 979), by Mr. Kenneth W. Simonds may well represent another species of *Pterodrilus*. These specimens appear to differ from those of other species of *Pterodrilus* in that there are three or four prongs of the dorsal projection on segment VIII, there appear to be dorsal ridges without projections on the other segments, and the prostate seems to be undifferentiated with a a thick-walled "prostatic bulb." The latter two points cannot be confirmed in my material, which raises the question as to whether the differences in the number of prongs of the dorsal projection may not be due to intraspecific variability in *P. hobbsi*. If the prostate should be differentiated and there are no dorsal ridges other than that bearing the projection on segment VIII, these animals could be distinguished from *P. hobbsi* only by the number of prongs of the dorsal projection. Better preserved material will almost surely show that these specimens represent a new species, but I am unwilling to describe a species on the basis of such poor material.

These specimens are from the following localities in the upper Hiwassee drainage: Union County, Ga., 2.6 miles east of the Fannin County line on U.S. Highway 76, hosts *Cambarus latimanus* (LeConte), *C. bartonii bartonii* (Fabricius), Nov. 5, 1958, K. W. Simonds, coll. (PCH 915); Union County, Ga., 0.5 mile north of Vogel State Park on U.S. Highway 19, hosts *Cambarus longulus longirostris* Faxon, *C. carolinus* Erichson, *Cambarus* species, Nov. 5, 1958, K. W. Simonds, coll. (PCH 979); Cherokee County, N.C., 1.4 miles off Joe Brown Road, in Grape Creek, hosts *Cambarus bartonii bartonii* (Fabricius), *Cambarus* species, June 6, 1959, K. W. Simonds, coll. (PCH 974).

Evolutionary Considerations

The genus *Pterodrilus* is a group of closely related species derived from a primitive stock of the genus *Cambarincola* that specialized in the direction of small size and presumably a relatively narrow niche on the crayfish host. It would be of considerable importance if we knew more precisely what this niche is. Brown (1961, p. 25) has shown that *P. alcicornus* is randomly distributed over the ventral surface of the hosts. The other species of the genus almost surely

occupy the same microhabitat. Diatoms make up a goodly part of the food of the species of *Pterodrilus* and they inhabit creeks and branches in upland regions, but nothing else is known about their ecological requirements. One is forced, then, to discuss their primitive characteristics and their subsequent specializations as adaptations fitting them for unknown ways of life. I shall proceed by describing the

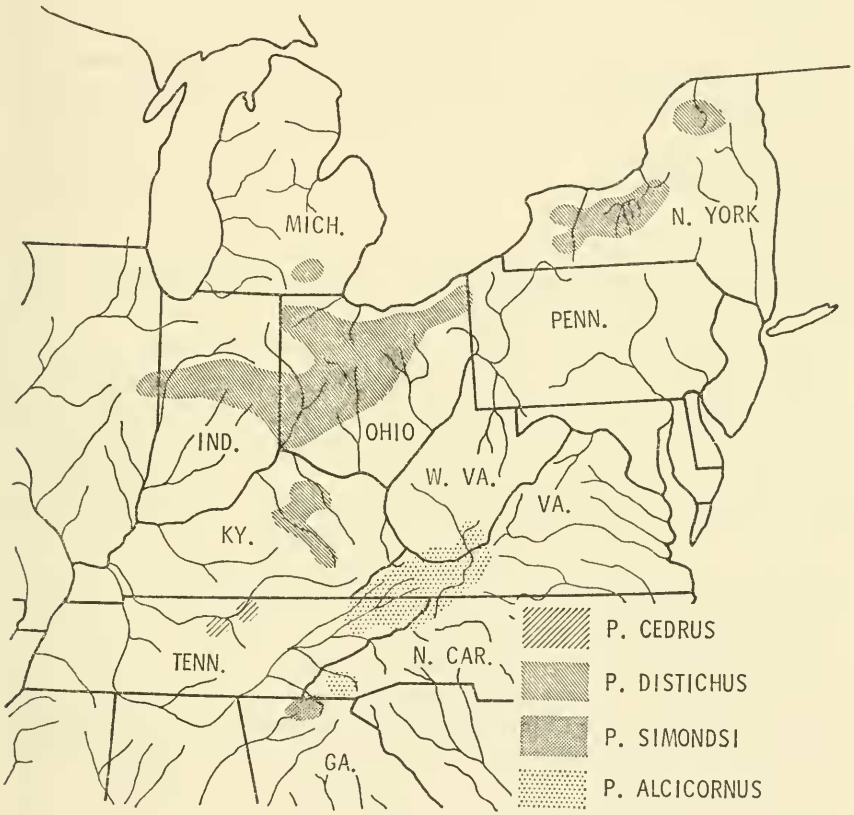

FIGURE 10.—Distribution of certain species of *Pterodrilus*.

hypothetical primitive pro-pterodrilus as I conceive it to have been and by defending, along the way, the reasons its various characteristics must be considered primitive. From these hypothetical considerations a tentative phylogeny will be derived and this in turn will be tested against the distributional data. Thus, a reasonable, if not necessarily true, story of the evolution of the genus can be written.

THE PRIMITIVE *PTERODRILUS*.—The ancestors of *Pterodrilus* were the smallest of the North American branchiobdellids, not

greatly, if at all, exceeding 2.0 mm in length. As branchiobdellids go, they were graceful animals, and their size was probably an adaptation that enabled them to escape competition with their larger relatives by retreating farther into the smaller crevices found on the underside of a crayfish than their relatives could and there exploiting the food found in such crannies.

The dorsum of the prosomite of segment VIII on these animals was raised into a ridge by the existence of supernumerary muscles. Such ridges are found on the prosomites of one or several segments of a number of branchiobdellids in genera that are not closely related to *Pterodrilus*, as well as among the species of the genera *Cambarincola* and *Oedipodrilus* Holt (1967a, p. 58). Perhaps this arrangement of the body-wall musculature is related in a mechanical sense to the hirudinoid mode of locomotion adopted by the branchiobdellids. One might conclude, then, that the absence of these ridges on all segments other than segment VIII is a primitive condition and that the evolutionary trend in *Pterodrilus* has been in the direction of an increasing number of such ridges.

The tendency in the genus *Pterodrilus* for the dorsal ridges to bear projections of unknown adaptive significance is shared with *Ceratodrilus* and the Asian *Cirrodrilus*, genera that are dissimilar to *Pterodrilus* in most other respects. The primitive progenitor of *Pterodrilus* lacked these projections, as the species *P. missouriensis* and *P. choritonamus* attest. In spite of our ignorance of the adaptive significance of these projections, it is assumed that the species with few or none are more primitive in this respect than are those with dorsal projections on several segments.

The jaws of pro-pterodrilus were generally small and delicate in appearance: the upper bore five teeth; the lower, four. Except for the reduction in size, this is the usual, and probably primitive, pattern in the genus *Cambarincola* and that found in all species of *Pterodrilus*. The cylindrical body shape, common anterior nephridiopore and 5/4 dental formula are features shared by *Pterodrilus* and *Cambarincola* and hence by the progenitor of *Pterodrilus*.

The innermost parts of the male reproductive system are basically the same in all branchiobdellids (Holt, 1965, p. 26) and nothing needs to be said about the testes in segments V and VI, the efferent funnels and ducts, or the deferent ducts. The spermiducal gland received the deferent ducts entally without the deferent lobes (Hoffman, 1963, p. 286) that are found in some putatively primitive species of *Cambarincola*. The gland had a lesser relative diameter and a proportionally greater length than that in all the species of today except *P. missouriensis* and, to a lesser extent, *P. mexicanus*.

The prostate was a small gland, about ⅓ the length of the spermiducal gland, that arose about ⅓ the latter's length from its junction with the ejaculatory duct. The prostate of the more advanced species of *Cambarincola* and *Pterodrilus* is differentiated. In pro-pterodrilus it was undifferentiated and consisted of a lobe of glandular epithelium that was histologically indistinguishable from that of the spermiducal gland. There may have been a prostatic "bulb" at the ental end that consisted of a few differentiated cells. In more advanced species of *Cambarincola*, the bulb is a distinctive and specialized part of the prostate. In all species of *Pterodrilus* the lumen of the prostate opens into that of the spermiducal gland some distance entad to the junction of the latter with the ejaculatory duct. In *Cambarincola*, the prostate and spermiducal gland usually open together into the ejaculatory duct. That the prostatic glands of the two genera are homologous cannot be doubted, but that of *Pterodrilus* is closer in this respect than is *Cambarincola* to *Ceratodrilus* Hall (Holt, 1960a, p. 57), *Ellisodrilus* Holt (1960b, p. 172), and *Oedipodrilus* Holt (1967a, p. 58). The latter genera must on this account and others be considered as primitive relatives of *Cambarincola*. The histological differentiation of the prostate occurs in the more advanced species of both *Cambarincola* (Hoffman, 1963, pp. 287, 301, et seq.) and *Pterodrilus* (only *P. missouriensis* has a completely undifferentiated prostate). The evolutionary trend in the specialization of the prostate seems to be clear.

The ejaculatory duct was probably short; though this supposition is based upon the length of the ejaculatory duct of *P. mexicanus*, it is strengthened by the fact that in the presumably primitive genera of the branchiobdellids, the ejaculatory duct is absent or short (Holt, 1968).

The bursa of pro-pterodrilus was proportionally larger than that found in *Cambarincola* and all the pterodrilids except *P. missouriensis* and *P. mexicanus*. The penial sheath region of the bursa may not have been unusually large, but the penis may have been partially eversible. This conjecture is based upon the opinion (Holt, 1968) that the primitive members of the lineage leading to *Cambarincola* and *Pterodrilus* possessed an eversible as opposed to a protrusible penis. The known members of this lineage (*Magmatodrilus* Holt, 1967b, and an unnamed Mexican genus), which lack a prostate, possess a bursa with a large penial sheath enclosing an eversible or semi-eversible penis; those (*Oedipodrilus* and *Ceratodrilus*) with incompletely separated prostates likewise have large bursae with eversible penes. Arguments based on the spacial relationships of the set of tubes that is the male reproductive system of the branchiobdellids and the conditions in other annelids have been set forth elsewhere

(Holt, 1968) supporting the hypothesis that an eversible penis, as opposed to the protrusible one, is primitive. If these arguments be allowed, it would be expected that pro-pterodrilus may have been provided with a penis that was proportionally longer and less in diameter than the cone-shaped one of *Cambarincola*. Such a penis is found in *P. missouriensis*, *P. mexicanus*, and *P. choritonamus*.

The spermatheca had an ectal duct that was heavily muscular and entally expanded at its junction with the spermathecal bulb, which in turn was provided with a muscular wall or a thick lining of tall collumnar epithelial cells. There may have been an ental process, but in any case the spermatheca consisted of more diverse elements than the simple muscular tube that is the spermathecal duct and the thin-walled expanded bulb without an ental process characteristic of the advanced members of the genus and of *Cambarincola*. This opinion is based upon conditions in related but more primitive genera (Holt, 1960a, 1967b, 1968) and upon a consideration of conditions in what are otherwise thought to be primitive species of *Pterodrillus*, i.e., those with an undifferentiated prostate.

A PHYLOGENY OF THE GENUS *PTERODRILUS*.—Except that it has low dorsal ridges on segments I to VII and that the spermatheca varies in ways difficult to evaluate, *P. missouriensis* fits remarkably well the above description of the primitive *Pterodrilus*. But three other species form with this one a group of primitive phylogenetic relicts in the genus: *P. choritonamus*, *P. mexicanus*, and *P. cedrus*. The major problem remaining in the attempt to reconstruct the history of the genus is that of convergence. If one bases a proposed phylogeny on the evolution of dorsal ridges and projections, a quite satisfactory scheme is produced except that there are two distinct lineages of which the more advanced members of each have very similar reproductive systems. Conversely, a phylogeny based on the evolution of the reproductive systems produces a phylogenetic dendrogram that is almost a straight line and places closely together such species as *P. hobbsi* and *P. alcicornus* that otherwise are unlike. The solution has been a modified compromise (fig. 11) that assumes a condiserable degree of convergence in the evolution of the reproductive systems, mostly because the alternative would suggest that at least some limeages alternately acquired and lost dorsal ridges and projections, an inherently improbable hypothesis.

Two levels of structural specialization were reached in the evolution of *Pterodrilus* and two minor radiations occurred. Four species (*P. missouriensis*, *P. choritonamus*, *P. mexicanus*, and *P. cedrus*) compose a group, derived from the original pro-pterodrilus stock, that is characterized by primitive features of the reproductive system and dorsal projections on only one segment or none at all. From the

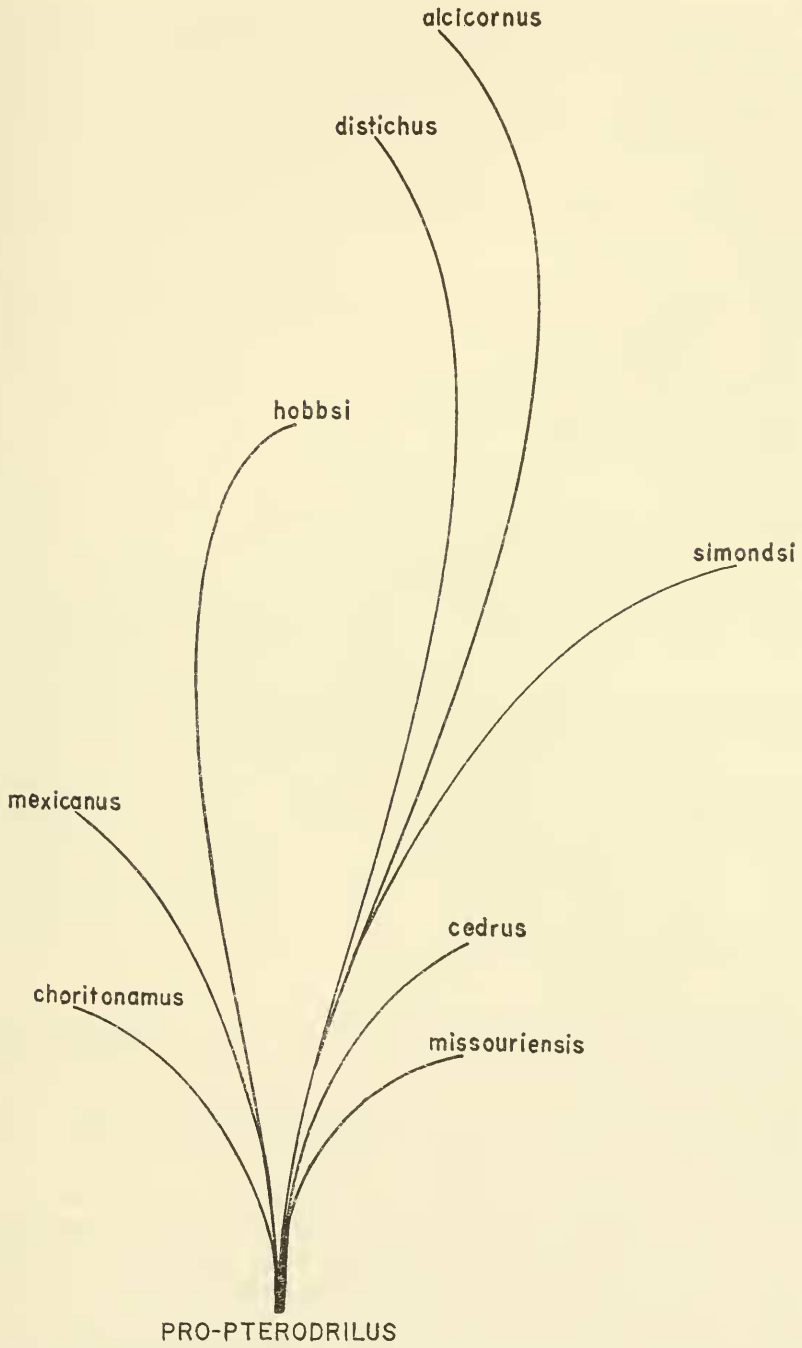

FIGURE 11.—A phylogeny of the genus *Pterodrilus*.

radiation that produced these species, a form similar to *P. mexicanus* gave rise to *P. hobbsi*, which evolved a more advanced type of reproductive system and stands at the second evolutionary level. *Pterodrilus cedrus* is the survivor of a stock with dorsal ridges and projections that gave rise to the other main lineage composed of *P. distichus*, *P. alcicornus*, and, at a more primitive stage of the development of the reproductive systems, *P. simondsi*, the members of the second radiation.

Places of origin and migrations.—When the distribution of the species of *Pterodrilus* (figs. 9, 10) is considered along with the hypothesis of their phylogeny that has been sketched here, some conclusions immediately emerge. The phylogenetically primitive species are scarce and localized. The most primitive of all, *P. missouriensis*, is known from a single location in the headwaters of the Gasconade River in Missouri. The more abundant but still relatively scarce *P. mexicanus* is essentially confined to the White River system in Missouri and Arkansas since it is otherwise known only from the nearby St. Francis River in Missouri, a tributary to the Arkansas River in Oklahoma, and Veracruz, Mexico. *Pterodrilus choritonamus* and *P. cedrus* are inhabitants of tributaries to the Cumberland River in the Eastern Highland Rim and Nashville Basin regions of Tennessee, *P. hobbsi* is a widespread and successful species of the Cumberland and Tennessee River systems with outliers in the Big Sandy and New Rivers. Of the species of the lineage with dorsal projections on multiple segments, the most primitive, *P. simondsi*, is localized in the Hiwassee River drainage of the Tennessee basin; *P. distichus* is a species of the Kentucky River that has crossed the Ohio to invade the eastern Great Lakes and St. Lawrence drainages; *P. alcicornus* is found in the Tennessee and New River systems, again with outliers to the east and north in the Savannah, Roanoke, James, and Big Sandy Rivers.

The ancestral home of the genus *Pterodrilus* most likely is in the headwaters of the Cumberland River in the Eastern Highland Rim region of Tennessee. Two of the four most primitive species, *P. choritonamus* and *P. cedrus*, still persist as phylogenetic and geographic relicts in this region. The other species are arranged radially around this center in a fashion that almost requires that their ancestors come from the Cumberland (fig. 12).

The same general region was the postulated home of the ancestors of the host animals, primitive *Procambarus* crayfishes that gave rise to the genera *Orconectes* and *Cambarus*, with *Orconectes* spreading mostly to the north and west, *Cambarus* to the east and south, and some stocks of *Procambarus* southwestward into Mexico (Hobbs, 1967, p. 15). The modern host relationships of species of *Pterodrilus* can

afford little insight into the problems of evolution and migrations of either the hosts or their epizoites: it is well established (Goodnight, 1940, p. 65; Hobbs, Holt, and Walton, 1967, p. 75) that host specificity in the classical sense of a species-to-species correspondence does not occur. Yet it is worthy of note that the crayfish-branchiobdellid associations as recorded under "Hosts" for each species is consistent with the hypothesis that *Pterodrilus* originated in the Cumberland basin and spread from there with the ancestors of the hosts of today, mostly species of *Orconectes*.

An attempt is made (fig. 12) to diagram more precisely the geo-

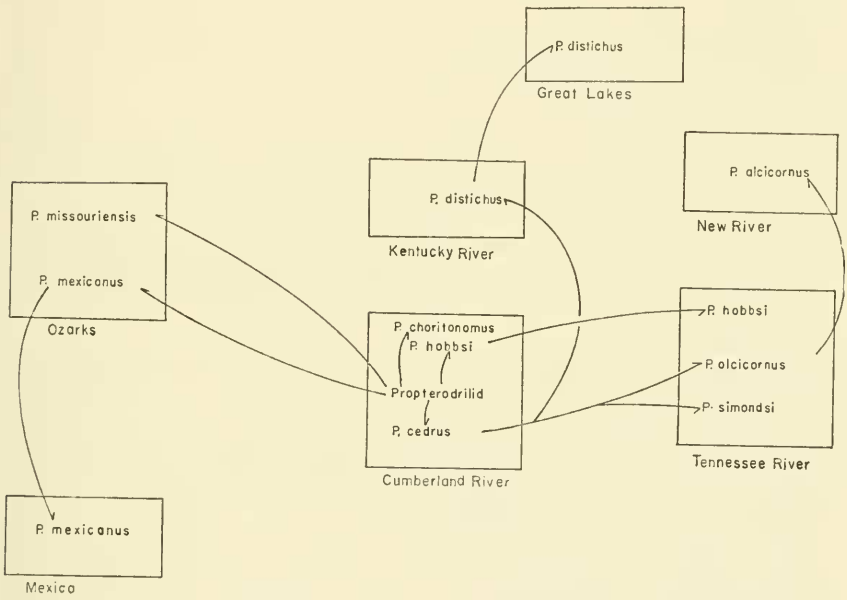

FIGURE 12.—The evolution of the genus *Pterodrilus*.

graphical relationships of the species of *Pterodrilus*. The times at which all these migrations occurred cannot be determined on the basis of the evidence now available, but the original diversification of the early *Pterodrilus* stock took place well back in the Tertiary, and the movement of *P. distichus* into the glaciated regions of the north, of necessity, has happened since the last glaciation. Without attempting to pinpoint the events in time on the basis of the hypothesis developed, we can note that an early diversification of pro-pterodrilus stocks occurred in the Cumberland basin. Of this radiation, *P. choritonamus* and *P. cedrus* remain in the general area of their ancestral home as relict forms. A primitive species, represented today by *P. missouriensis*, moved early into the northward-flowing streams of the Missouri

Ozarks. Whether *P. mexicanus* is a descendant of this stock that moved over the Ozarkian divide into the White River and adjacent drainages cannot be determined with certainty: the postulated phylogeny suggests that it likewise came into the Ozarks by the same route, but if so, it seems somewhat strange that it is unknown from the Missouri basin. Yet few collections have been taken from the northern Ozarks in Missouri, and further field work may well reveal the presence of *P. mexicanus* there. But *P. mexicanus* is obviously extinct over much of the route it or its ancestral form must have taken to reach the Ozarks, and the same or similar factors that caused this restriction of range may operate in the streams of the Missouri River system in southern Missouri. It is not surprising that an early stock of *Pterodrilus* may have moved into Mexico: the crayfish hosts did so sometime before the end of the Miocene (Hobbs, 1967, p. 15). The possibility remains that the Ozarkian worms are not conspecific with the type of *P. mexicanus* (see p. 18 above), but any solution of the problem of the status of P. *mexicanus* will fit these ideas; for if it is recovered from Mexico and a new name assigned to my specimens from the Ozarks, the Mexican worms are, on the basis of my study of the type, very similar to the Ozarkian ones. Such a solution, however, would date the early migrations of *Pterodrilus* stocks in the Miocene or earlier (Hobbs, 1967, p. 15).

Turning now to the north and east, we note that there are large gaps in the range of *P. distichus* (fig. 10) that can only be attributed to inadequate collecting. The records from the Kentucky and Licking Rivers are near the postulated place of origin of the species and may represent the Pleistocene refugium from which *P. distichus* has moved north and northeastward, most likely by way of the Miami and Scioto Rivers, since the Wisconsin glaciation. The gap in the range of *P. distichus* in the Lake Erie basin in Pennsylvania and New York surely represents inadequate collecting.

Pterodrilus hobbsi has arisen from a stock that also produced *P. mexicanus*, but it has reached a higher level of development in the structures of the reproductive systems. Its sympatry with its primitive relative *P. choritonamus* argues for its origin in a part of the Cumberland basin, perhaps the headwaters of the Cumberland in southeast Kentucky, not inhabited by the latter and a reinvasion of the homeland. From such a region, the invasion of the Tennessee basin, where *P. hobbsi* is widespread and successful, of the Big Sandy, and of the New River is entirely possible. There are, however, gaps in its known range, and other histories of the species are possible. Its absence from the central part of the Cumberland Plateau in Tennessee appears to be real, but further collecting can be expected

to connect the parts of its range that now appear to be disjunct. If so, the upper reaches of the Cumberland in Kentucky remain the likely site of origin for *P. hobbsi*. The few scattered records from the Big Sandy and the New Rivers indicate that the species is still actively extending its range, and much of the spreading of *P. hobbsi* may well have occurred quite recently.

The migrations of *P. distichus*, *P. hobbsi*, and *P. alcicornus* may have occurred rather recently, but the movement of the stock that gave rise to *P. simondsi* must be older. Although it is believed that a common ancestor gave rise to both *P. simondsi* and *P. alcicornus*, the former clearly stands at a lower level of evolutionary advance as is indicated by the primitive nature of its reproductive systems. It is known only from the tributaries to the Ocoee River and one locality in the Nottely, both parts of the Hiwassee River system of the Tennessee River basin. *Pterodrilus simondsi* is found, then, at the southeastern periphery of the range of the genus in an isolated part of the somewhat isolated Hiwassee basin. Its ancestors came from the Cumberland and its known distribution can be explained by postulating that the species was once widespread in the Tennessee basin but has been eliminated throughout all of its range except the small part in the Hiwassee by the more advanced, successful, and widespread species, *P. hobbsi* and *P. alcicornus*. In any case, though the origins of *P. simondsi* may not be as ancient as those of the relict species in middle Tennessee and the Ozarks, it is an older relative of *P. alcicornus* holding out in a relict status in a part of the Tennessee basin not yet successfully invaded by the latter.

If the *hobbsi*-like animals mentioned above (p. 32) are conspecific with other populations of *P. hobbsi*, the Hiwassee drainage is being invaded by this more advanced species, but if, as seems more likely, these specimens represent a survival of the primitive stock that gave rise to *P. cedrus*, we have at the periphery of the present range of the genus a relict of the first radiation within *Pterodrilus*.

Pterodrilus alcicornus is the most advanced and successful species of the genus. It is a native of the New River basin that has in recent times extended its range, probably by stream captures, into the James and Roanoke basins to the east, into the Big Sandy to the north, and, amazingly, into the Savannah in the south. The latter invasion can only have occurred by means of the streams of the Tennessee system that lie between the headwaters of the New and the Savannah in western North Carolina, a region that has been inadequately sampled. Still earlier, *P. alcicornus* had moved into the upper reaches of the Tennessee River system in southwestern Virginia and northeastern Tennessee, where it is sympatric with *P. hobbsi*, often occupy-

ing the same streams and presumably the same hosts. A *cedrus*-like stock that gave rise to *P. distichus* to the north and a more primitive member, *P. simondsi*, to the south, moved by way of former connections with the Cumberland into the New River basin to produce *P. alcicornus*.

The history of the genus *Pterodrilus* is conceived in broad outline, then, to be like this: In early Miocene or pre-Miocene times a primitive stock of cambarincoloid branchiobdellids were epizoites carried by the progenitors of the modern crayfish fauna of the upland regions of eastern North America. These animals lived along the slopes of the present Appalachian uplift, represented today by the Cumberland Plateau and the Highland Rim, which was drained by a stream that corresponded to the present day Cumberland. From this center, early stocks moved into the Ozarks and perhaps on into Mexico with the progenitors of the Mexicanus Section of the crayfish genus *Procambarus* (Hobbs, 1967, pp. 13–15) and produced the species *P. missouriensis* and *P. mexicanus*. *Pterodrilus choritonamus* and *P. cedrus* are the survivors (and representatives of the two lineages produced) of this early diversification that remained in the area of their origin and *P. hobbsi* is a more advanced member of the *choritonamus-mexicanus* lineage that has not only remained in the Cumberland basin but has successfully invaded the Tennessee system and more recently the New River drainage. Some of the early members of the *missouriensis-cedrus* lineage have also moved eastward, with one and possibly two (*P. simondsi* and the unnamed animals) remaining today in the Hiwassee basin as relicts. This lineage also gave rise to the advanced species, *P. alcicornus*, in the New River basin. Moving to the north, most likely by way of the Kentucky River or a nearby stream, another branch of this lineage gave rise to *P. distichus*, which remained in the Kentucky region throughout the Pleistocene, and in Recent times has followed its crayfish hosts (primarily species of *Orconectes*) into the Great Lakes and the St. Lawrence basins.

These migrations have left three regions in which primitive species remain today: the original home, the Cumberland basin; the Ozarks in the Missouri and Arkansas river systems (and possibly the eastern slopes of the Sierra Madre Oriental in Veracruz); and the Hiwassee basin along the southwestern slope of the Blue Ridge. Of the dominant members of the genus, *P. hobbsi* is a product of the original diversification in the Cumberland that today is most successful in the Tennessee basin; while of a second radiation of the *P. cedrus* lineage, *P. distichus* has invaded the recently glaciated areas to the north, and *P. alcicornus* has made its principal home in the valley of the New River.

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